EDGE-EFFECTS IN CANOPY ARTHROPODS OF *PICEA SITCHENSIS*
AND *PINUS SYLVESTRIS* PLANTATIONS IN THE UK.

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The present research aims to establish the depth of abiotic and invertebrate edge-effects occurring in plantations of two conifer species, and the resulting effects of management practices on ‘edge’ and ‘core’ invertebrate communities. Near complete invertebrate samples were collected using chemical knockdown allowing analysis of invertebrates at the order, family, genus, species and guild level.

Similar invertebrate densities per m² ground area occurred in both tree species, although communities differed between them, *Pinus sylvestris* supporting a more diverse community than *Picea sitchensis*. Species richness, diversity and densities varied with distance from plantation edge with the Acarina, Araneae, Coleoptera, Collembola, Diptera and Hemiptera showing particularly strong responses to edge proximity.

Abiotic edge-effects, although variable between transects, occurred to an average depth of 30 metres with an approximate 1°C drop in temperature and a 5% increase in relative humidity towards the core. Invertebrate edge-effect depths varied with species, ranging from 5 to 80 metres. In *P. sitchensis* invertebrate richness and densities, particularly for Coleoptera, Araneae and Hemiptera were higher in the edge habitat, whilst increased richness and diversity occurred in the core of *P. sylvestris*.

Edge habitat is key to optimising richness in *P. sitchensis*, however application of core-area models shows that current plantation management fails to maximise edge habitat. Reduction of patch size and/or increasing edge features will increase species richness. In contrast core habitat is vital to species richness in *P. sylvestris*. Current small patch size limits invertebrate richness, increased patch size and implementation of edge buffer zones would protect core habitat thus enhancing invertebrate species richness.
**Contents.**

Abstract .................................................................................................................................. 1
Contents................................................................................................................................II
List of Figures ..................................................................................................................... VI
List of Tables .................................................................................................................... XIII
Acknowledgements ........................................................................................................ XVII

Chapter 1. Introduction ................................................................................................ 1

Chapter 2. Methodology .................................................................................................. 19
  2.1 Introduction .............................................................................................................. 19
  2.2 Tree species .............................................................................................................. 24
  2.3 Site selection ............................................................................................................. 27
  2.4 Transects .................................................................................................................... 29
  2.5 Abiotic sampling ....................................................................................................... 32
  2.6 Invertebrate sampling .............................................................................................. 33
    2.6.1 Chemical knockdown ................................................................................... 33
    2.6.2 Mistblowing .................................................................................................. 37
    2.6.3 Sampling protocol ......................................................................................... 39
    2.6.4 Invertebrate data handling ............................................................................ 43
    2.6.5 Guild classification ....................................................................................... 47

Chapter 3. Edge-effects .................................................................................................. 51
  3.1 Introduction ............................................................................................................... 51
  3.2 Methods .................................................................................................................... 58
  3.3 Results ....................................................................................................................... 63
    3.3.1 Humidity edge-effects ................................................................................... 63
    3.3.2 Temperature edge-effects ............................................................................ 71
    3.3.3 Invertebrate edge-effects ............................................................................. 79
      3.3.3.1 Positive mean density responses to edge ......................................... 79
Chapter 3. Edge-Effects

3.3.2 Positive species richness and diversity responses to edge
3.3.3 Positive guild responses to edge
3.3.4 Negative mean density responses to edge
3.3.5 Negative species richness and diversity responses to edge
3.3.6 Negative guild responses to edge
3.3.4 Squared and relative euclidean distance edge-effects
3.3.4.1 Abiotic data
3.3.4.2 Positive invertebrate responses to edge
3.3.4.3 Negative invertebrate responses to edge

3.4 Discussion
3.4.1 Abiotic edge-effects
3.4.2 General invertebrate edge-effects
3.4.3 Coleoptera edge-effects
3.4.4 Dipteran edge-effects
3.4.5 Araneae edge-effects
3.4.6 Collembolan edge-effects
3.4.7 Acarina edge-effects
3.4.8 Conclusions

Chapter 4. Core-Area Models
4.1 Introduction
4.1.1 Patch size
4.1.2 Patch shape
4.1.3 Size and shape models
4.1.4 Core-area models
4.2 Methods
4.2.1 Research patches
4.2.2 Management patches
4.3 Results
4.3.1 Research patches
4.3.1.1 Humidity core areas ................................................................. 170
4.3.1.2 Temperature core areas ............................................................ 174
4.3.1.3 Abiotic squared euclidean distance core areas ......................... 176
4.3.1.4 Invertebrate core areas ............................................................. 178
4.3.1.5 Invertebrate squared and relative euclidean distance core areas .. 180
4.3.2 Management patches ................................................................. 181
  4.3.2.1 Picea sitchensis ................................................................. 183
  4.3.2.2 Pinus sylvestris ................................................................. 187
4.4 Discussion ..................................................................................... 191
  4.4.1 Picea sitchensis patches ............................................................ 192
  4.4.2 Pinus sylvestris patches ............................................................ 197
  4.4.3 Application of the core-area model ........................................... 202

Chapter 5. Tree species ........................................................................ 206
5.1 Introduction ................................................................................... 206
  5.1.1 Plant / Invertebrate abundance ................................................. 207
  5.1.2 Plant chemistry ................................................................. 211
  5.1.3 Plant architecture ............................................................... 213
  5.1.4 Canopy microclimate ........................................................... 218
  5.1.5 Regional climate ................................................................. 220
5.2 Methods ....................................................................................... 223
5.3 Results ......................................................................................... 226
  5.3.1 Abiotic data ................................................................. 226
  5.3.2 Mean densities ................................................................. 226
  5.3.3 Mean species richness ......................................................... 227
  5.3.4 Invertebrate species ............................................................. 232
    5.3.4.1 Acarina ................................................................. 233
    5.3.4.2 Araneae ................................................................. 234
    5.3.4.3 Coleoptera ........................................................... 239
  5.3.5 Invertebrate percentage abundances ....................................... 241

IV
List of Figures.

Chapter 3.

Figure 3.1. Mean values of (A) relative humidity (%) and (B) temperature (°C) against distance (m) from plantation edge for combined *Picea sitchensis* transects.

Figure 3.2. Mean values of (A) relative humidity (%) and (B) temperature (°C) against distance (m) from plantation edge for *Picea sitchensis* transect 1.

Figure 3.3. Mean values of (A) relative humidity (%) and (B) temperature (°C) against distance (m) from plantation edge for *Picea sitchensis* transect 2.

Figure 3.4. Mean values of (A) relative humidity (%) and (B) temperature (°C) against distance (m) from plantation edge for *Picea sitchensis* transect 3.

Figure 3.5. Mean values of (A) relative humidity (%) and (B) temperature (°C) against distance (m) from plantation edge for *Picea sitchensis* transect 4.

Figure 3.6. Mean values of (A) relative humidity (%) and (B) temperature (°C) against distance (m) from plantation edge for combined *Pinus sylvestris* transects.

Figure 3.7. Mean values of (A) relative humidity (%) and (B) temperature (°C) against distance (m) from plantation edge for *Pinus sylvestris* transect 1.

Figure 3.8. Mean values of (A) relative humidity (%) and (B) temperature (°C) against distance (m) from plantation edge for *Pinus sylvestris* transect 2.

Figure 3.9. Mean values of (A) relative humidity (%) and (B) temperature (°C) against distance (m) from plantation edge for *Pinus sylvestris* transect 3.
Figure 3.10. Mean coleopteran density (m$^2$) in combined *Picea sitchensis* edge (0-10m) and core (80-120m) samples (P=0.016 indep. t-test).

Figure 3.11. Mean *Aphipecta obliterata* (Coleoptera) density (m$^2$) in block *Picea sitchensis* edge (0-10m) and core (80-120m) samples (P=0.003 indep. t-test).

Figure 3.12. Mean coleopteran species richness (m$^2$) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples (P=0.034 indep. t-test).

Figure 3.13. Mean dipteran density (m$^2$) in transect 3 *Picea sitchensis* edge (0-10m) and core (80-120m) samples (P=0.014 indep. t-test).

Figure 3.14. Mean dipteran density (m$^2$) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples (P=0.027 indep. t-test).

Figure 3.15. Mean hemipteran density (m$^2$) in transect 4 *Picea sitchensis* edge (0-10m) and core (80-120m) samples (P=0.001 indep. t-test).

Figure 3.16. Mean Linyphiidae (Araneae) density (m$^2$) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples (P=0.04 indep. t-test).

Figure 3.17. Mean collembolan density (m$^2$) in transect 2 *Picea sitchensis* edge (0-10m) and core (80-120m) samples (P=0.037 indep. t-test).

Figure 3.18. Mean collembolan density (m$^2$) in combined *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.031 indep. t-test).

Figure 3.19. Mean *Sminthurus juscus* (Collembola) density (m$^2$) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples (P=0.047 indep. t-test).

Figure 3.20. Mean total invertebrate species richness (m$^2$) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples (P=0.000 indep. t-test).
Figure 3.21. Mean Acarina species richness (m$^2$) in combined *Picea sitchensis* edge (0-10m) and core (80-120m) samples (P=0.022 indep. t-test).

Figure 3.22. Mean Acarina species richness (m$^2$) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples (P=0.000 indep. t-test).

Figure 3.23. Mean tourist guild densities (m$^2$) with distance from plantation edge (m) for *Picea sitchensis* transects.

Figure 3.24. Mean tourist guild densities (m$^2$) with distance from plantation edge (m) for *Pinus sylvestris* transects.

Figure 3.25. Mean species richness (m$^2$) of Acarina detritivores between edge (0-10m) and core (80-120m) samples in *Picea sitchensis* plantations (P=0.000 indep. t-test).

Figure 3.26. Mean species richness (m$^2$) of Acarina predators between edge (0-10m) and core (80-120m) samples in *Picea sitchensis* plantations (P=0.000 indep. t-test).

Figure 3.27. Mean species richness (m$^2$) of Coleoptera herbivores between edge (0-10m) and core (80-120m) samples in *Picea sitchensis* plantations (P=0.001 indep. t-test).

Figure 3.28. Percentage contribution of Coleoptera guild densities (m$^2$) to (A) edge (0-10m) and (B) core (80-120m) communities of combined *Pinus sylvestris* samples.

Figure 3.29. Mean *Entomobrya nivalis* (Collembola) density (m$^2$) in transect 2 *Picea sitchensis* edge (0-10m) and core (80-120m) samples (P=0.034 indep. t-test).

Figure 3.30. Mean Acarina density (m$^2$) in transect 1 *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.041 indep. t-test).

Figure 3.31. Mean collembolan density (m$^2$) in transect 3 *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.001 indep. t-test).

Figure 3.32. Mean *Entomobrya nivalis* (Collembola) density (m$^2$) in transect 3 *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.001 indep. t-test).
Figure 3.33. Mean *Drapetisca socialis* (Araneae) density (m$^2$) in combined *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.032 indep. t-test).

Figure 3.34. Mean *Lepthyphantes expunctus* (Araneae) density (m$^2$) in transect 2 *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.013 indep. t-test).

Figure 3.35. Mean neuropteran density (m$^2$) in combined *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.041 indep. t-test).

Figure 3.36. Mean Acarina species richness (m$^2$) in combined *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.022 indep. t-test).

Figure 3.37. Mean Acarina species richness (m$^2$) in transect 1 *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.003 indep. t-test).

Figure 3.38. Mean species richness (m$^2$) of Acarina detritivores between edge (0-10m) and core (80-120m) samples in *Pinus sylvestris* plantations (P=).

Figure 3.39. Mean squared euclidean distance (SED) plotted against distance (m) for combined *Picea sitchensis* transect abiotic data, showing highest contrast between 0 and 5 metre samples.

Figure 3.40. Mean squared euclidean distance (SED) plotted against distance (m) for *Picea sitchensis* transect 1 abiotic data, showing areas of high contrast over the first 30 metres.

Figure 3.41. Mean squared euclidean distance (SED) plotted against distance (m) for *Picea sitchensis* transect 3 abiotic data, showing highest contrast between 0 and 5 metre samples.

Figure 3.42. Mean squared euclidean distance (SED) plotted against distance (m) for *Pinus sylvestris* transect 1 abiotic data, showing points of high contrast at either end of the transect.

Figure 3.43. Mean squared euclidean distance (SED) plotted against distance (m) for *Pinus sylvestris* transect 2 abiotic data, showing high areas of contrast over the first 30 metres of the transect.
Figure 3.44. Mean relative euclidean distance (RED) plotted against distance (m) for *Picea sitchensis* transect 1 Acarina density (m²) data, showing high contrast between 0 and 5 metre samples.

Figure 3.45. Mean relative euclidean distance (RED) plotted against distance (m) for *Picea sitchensis* transect 2 Coleoptera density (m²) data, showing high contrast between 0 and 5 metre samples.

Figure 3.46. Mean squared euclidean distance (SED) plotted against distance (m) for *Picea sitchensis* transect 1 invertebrate diversity (Simpson’s index) data (m²), showing high contrast between 0 and 5 metre samples.

Figure 3.47. Mean squared euclidean distance (SED) plotted against distance (m) for *Pinus sylvestris* transect 2 invertebrate diversity (Simpson’s index) data (m²), showing high contrast over the first 20 metres.

Figure 3.48. Mean squared euclidean distance (SED) plotted against distance (m) for *Picea sitchensis* transect 1 Acarina species diversity (Simpson’s index) data (m²), showing high contrast between 0 and 5 metre samples.

Figure 3.49. Mean squared euclidean distance (SED) plotted against distance (m) for *Picea sitchensis* transect 4 Acarina species diversity (Simpson’s index) data (m²), showing high contrast between 5 and 10 metre samples.

Figure 3.50. Mean relative euclidean distance (RED) plotted against distance (m) for *Pinus sylvestris* transect 3 collembolan density data (m²), showing high contrast in the mid section of the transect.

Figure 3.51. Mean squared euclidean distance (SED) plotted against distance (m) for *Pinus sylvestris* combined transect invertebrate diversity (Simpson’s index) data (m²), showing high contrast between 80 and 90 metre samples.

Figure 3.52. Mean squared euclidean distance (SED) plotted against distance (m) for *Pinus sylvestris* transect 3 invertebrate diversity (Simpson’s index) data (m²), showing high contrast between 80 and 90 metre samples.
Chapter 4.

Figure 4.1. Diagram representing plantation edge management for the encouragement of edge invertebrates (Carter 1991, Greatorex-Davies 1991), showing relative loss of plantation area (shaded area) and perimeter length. A. Represents 10 and 20 metre Box junctions (Box 10 and Box 20) cut into the corners of forest patches. B. Represents high densities of 10 x 30 metre Bays cut into plantation edges every 30 metres (Bay 1). C. Represents low density 10 x 30 metre Bays (Bay 2) cut every 60 metres along plantation edges.

Chapter 5.

Figure 5.1. Mean lepidopteran density (m^2) between *Picea sitchensis* and *Pinus sylvestris* samples (P=<0.05).

Figure 5.2. Mean invertebrate species richness (m^2) between *Picea sitchensis* and *Pinus sylvestris* samples (P=<0.05).

Figure 5.3. Mean coleopteran species richness (m^2) between *Picea sitchensis* and *Pinus sylvestris* samples (P=<0.001).

Figure 5.4. Comparison of coleopteran family mean densities (m^2) between *Pinus sylvestris* and *Picea sitchensis* samples.

Figure 5.5. Percentage of total invertebrate abundance contributed by the major invertebrate orders for combined *Picea sitchensis* (A) and *Pinus sylvestris* (B) samples.

Figure 5.6. Mean guild percentages for combined *Picea sitchensis* (A) and *Pinus sylvestris* (B) samples.

Figure 5.7. Mean Acarina guild percentages for combined *Picea sitchensis* (A) and *Pinus sylvestris* (B) samples.

Figure 5.8. Mean predatory Acarina species richness (m^2) between *Pinus sylvestris* and *Picea sitchensis* samples (P=<0.000).

Figure 5.9. Mean coleopteran herbivore species richness (m^2) between *Pinus sylvestris* and *Picea sitchensis* samples (P=<0.000).
Figure 5.10. Mean Coleoptera guild percentages for combined *Picea sitchensis* (A) and *Pinus sylvestris* (B) samples.
List of Tables.

Chapter 2.

Table 2.1. Site and plantation details for all *Pinus sylvestris* and *Picea sitchensis* sample sites.

Table 2.2. List of taxa identified in mist blowing samples from the canopies of *Pinus sylvestris* and *Picea sitchensis* in the UK.

Table 2.3. Guild assignment for invertebrate taxa adapted from Moran and Southwood (1982) and Simandl (1983).

Chapter 3.

Table 3.1. Results of independent sample t-tests comparing mean edge (0-10m) and core (80-120m) relative humidity data (%) for combined and individual transects and block data, in *Picea sitchensis* and *Pinus sylvestris* plantations.

Table 3.2. Results of independent sample t-tests comparing mean edge (0-10m) and core (80-120m) temperature (°C) data, for combined and individual transects and block data, in *Picea sitchensis* and *Pinus sylvestris* plantations.

Table 3.3. Results of independent sample t-tests comparing mean invertebrate density (m²) between edge (0-10m) and core (80-120m) samples, for combined and individual transects, in *Picea sitchensis* and *Pinus sylvestris* plantations.

Table 3.4. Results of independent sample t-tests comparing mean species diversity scores (Simpson’s index) for total invertebrate capture and order level diversity in edge (0-10m) and core (80-120m) samples, for combined and individual transects, in *Picea sitchensis* and *Pinus sylvestris* plantations.

Table 3.5. Review of positive and negative invertebrate responses to edge proximity in *Picea sitchensis* and *Pinus sylvestris* plantations.
Table 3.6. Results of independent sample t-tests comparing mean guild density (m$^2$) of all arthropods between edge (0-10m) and core (80-120m) samples, for combined, individual transects and block data, in *Picea sitchensis*. No significant differences were seen in guild densities (m$^2$) between edge and core samples for *Pinus sylvestris* transects.

Table 3.7. Results of independent sample t-tests comparing mean coleopteran guild density (m$^2$) between edge (0-10m) and core (80-120m) samples, for combined, individual transects and block data, in *Picea sitchensis*. No significant differences were seen in coleopteran guild densities (m$^2$) between edge and core samples for *Pinus sylvestris* transects.

Chapter 4.

Table 4.1. Forest patch details for research patches in *Picea sitchensis* and *Pinus sylvestris*, required to calculate Shape Index (Patton 1975). Total area (TA) and patch perimeter (P) data obtained from Forestry Commission database and maps.

Table 4.2. Effects of hypothetical edge management on patch statistics required to calculate Shape Index (Patton 1975), for research patches in *Picea sitchensis* and *Pinus sylvestris*. Total area and patch perimeter data originally obtained from Forestry Commission database and maps, management effects calculated from map manipulation.

Table 4.3. Proportion of edge and core habitat (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for relative humidity (%) edge-effect depths in *Picea sitchensis* and *Pinus sylvestris* research patches.

Table 4.4. Proportion of edge and core habitat (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for temperature (°C) edge-effect depths in *Picea sitchensis* and *Pinus sylvestris* research patches.

Table 4.5. Proportion of edge and core habitat (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for abiotic squared euclidean distance(SED) edge-effect depths in *Picea sitchensis* and *Pinus sylvestris* research patches.
Table 4.6. Proportion of edge and core habitat (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for invertebrate density (m²) edge-effect depths in *Picea sitchensis* and *Pinus sylvestris* research patches.

Table 4.7. Proportion of edge and core habitat (hectares) and percentages for invertebrate squared and relative euclidean distances (S/RED), for density and diversity, in *Picea sitchensis* and *Pinus sylvestris* research patches.

Table 4.8. Proportion of edge and core habitat (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for mean edge-effect depths (5, 30 and 80 m) in *Picea sitchensis* plantations under various hypothetical edge management strategies.

Table 4.9. Proportion of edge and core habitat (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for mean edge-effect depths (5, 30 and 80 m) in *Pinus sylvestris* plantations under various hypothetical edge management strategies.

Chapter 5.

Table 5.1. Independent sample t-test results comparing mean densities (m²) of invertebrate taxon between *Picea sitchensis* and *Pinus sylvestris* plantations.

Table 5.2. Independent sample t-test results comparing mean species richness of invertebrate taxa (m²) between *Picea sitchensis* and *Pinus sylvestris* plantations.

Table 5.3. Acarina order and species list for *Picea sitchensis* and *Pinus sylvestris* samples.

Table 5.4. Araneae family and species lists for *Picea sitchensis* and *Pinus sylvestris* samples.

Table 5.5. Coleoptera family and species lists for *Picea sitchensis* and *Pinus sylvestris* samples.
Table 5.6. Independent sample t-test results comparing mean densities ($m^2$) of invertebrate guilds between *Picea sitchensis* and *Pinus sylvestris* plantations.
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Chapter 1. Introduction.

Ecology is a wide ranging discipline, at its most basic being the study of 'the interactions that determine the distribution and abundance of organisms' (Krebs 1972). However this definition fails to highlight the breadth of disciplines associated with the modern science of ecology, from the more traditional study of whole organisms and their populations to research into organisms at the cellular and molecular level and their evolution (Speight et al. 1999). The key to ecology is the attempt to elucidate the patterns and structure in populations and communities, in ecosystems and to define the environmental factors controlling these patterns. The understanding of the patterns in complex natural systems allows predictive work to follow, assessing the effects of management activity or global climate change on these patterns, providing the basis for conservation activity world wide.

The variations seen in communities and populations are irrevocably linked to the specific environment in which they are located. Aspects of the environment including both its physical and chemical (abiotic) properties and the presence of other organisms (biotic) inhabiting the area affect the communities and populations. Effects of these environmental factors on the organisms can be considered at many scales both within the ecosystem, such as at the leaf, branch, tree, forest, regional or global levels and also at the organism scale studying impacts on individuals, populations or communities.
Choice of habitat scale should be considered carefully depending on the research question, as habitats either at the landscape, regional or local scale affect organisms differently. Many recent studies have explored the landscape level effects of habitat distribution and fragmentation on animal communities, most particularly the positioning and connectivity of habitat patches within the landscape and the movement of organisms between them (Fahrig and Merriam 1985, Forman and Godron 1986, Simberloff et al. 1992, Drake et al. 1993, Andren 1994, Abensperg-Traun et al. 1996, Dudley and Adler 1996, Tiebout and Anderson 1997, Corbit et al. 1999, Mauritzen et al. 1999). Populations of organisms are considered to be more stable in a landscape with higher quantities of suitable habitat which are highly connected (Saunders et al. 1991, Andren 1994), with populations more likely to undergo fatal extinction events if highly isolated, due to reduced flow of individuals into the population (Blake and Karr 1984, Dale et al. 1994). Habitat fragmentation and disturbance has also been found to have an effect at the patch scale; patch size, shape and heterogeneity affecting the stability of populations within the patch (Chapter 3 and 4), with small convoluted and highly heterogeneous patches supporting more unstable communities (Janzen 1983, Blouin and Connor 1985, Forman and Godron 1986, Blake and Karr 1987, Andren and Angelstam 1988, Harrison et al. 1988). To study the effects of these two scales on organisms requires very different experimental design, the first requiring large scale sampling in many habitat patches and the corridors which connect them over long periods of time to assess either animal or genetic material flow between the areas. The second requires more detailed investigation of the populations within habitat patches of different sizes, shapes and areas for a short period of time.
The research question will also define the level of scale to be used for the organism, whether it is individuals, populations or communities (Richardson et al. 1997). Studies of individuals of a particular species in a habitat are commonplace, such research assessing the affects of the abiotic and biotic environment on the presence and absence of species within the habitat. These studies are of particular use for economically important species of insect (Speight and Wainhouse 1989, Speight et al. 1999) and provide information on the environmental conditions likely to initiate outbreak numbers, thereby allowing prediction of future outbreaks and the initiation of control mechanisms. The study of single species is also vital to many conservation initiatives, the detailed knowledge of their habitat requirements enabling appropriate management activities to be initiated.

However the concentration on single species can be limiting when considering more natural habitats and their diversity and conservation properties, here, the implementation of management practices based on a single species can result in damaging activity to other aspects of the community. But resources for conservation initiatives are often limited making base line research on all the organisms in the area impossible; therefore management centred on a single species is often the only possible solution. Afforestation of upland areas increased habitat diversity but led to a reduction in staphylinid beetle species that were not forest adapted such as *Quedius fuliginosus*, *Q. picipes* and *Drusilla canaliculata* (Buse and Good 1993). In similar situations management solely for forest species, i.e. the afforestation of the area, should not be implemented completely but a more integrated management system used varying tree species, age and open habitat area to encourage both forest and open habitat beetle species. A research study that simply
assessed the effects of afforestation on forest adapted staphylinid species would fail to highlight the reduction in open habitat species and therefore overall diversity of the habitat. Therefore communities in general provide a more useful tool than individuals in assessing the quality of a habitat for diversity purposes and the effects of changes in environmental factors or management on the area. The use of single species is only justified if the conservation initiative is an emergency or the proposed management is limited and likely to have few knock on effects on other aspects of the community.

Communities are a key concept in ecology (Begon et al. 1990) considered as the assemblages of species populations occurring together in space and time, the area of space being defined by the researcher. This artificial definition of the boundary of a community is often guided by the boundaries of a discrete habitat type, such as a forest canopy, or the common food source of a number of organisms. The study of communities assesses the patterns in the structure and interactions of these complex assemblages of species and the effects of the environment on them. Various properties of the communities are key to their study including the relative abundance of the species’ populations within the communities, their species diversity, richness and guild structure all of which will be used in the present research (Chapter 2).

The simplest way to classify a community is by the list of species it contains, its species richness (Southwood 1978, Begon et al. 1990) allowing comparison between different communities, however the technique suffers from limitations due to taxonomy and the necessity for standardising sample number, as number of species will increase with
sampling effort. The concept of species richness can be extended by including not only the number of species but also their rarity or commonness in a habitat, using diversity indices which describe the evenness of communities as well as their richness. Species richness fails to take into account the rarity and abundance of species occurring within an area, e.g. two communities may have an identical number of species but one community may have equal numbers of each species, while the other may have one species dominant over a number of rare species with few individuals. Although these two communities have the same species richness they are obviously different and diversity indices help to define their distinct characteristics.

A further, more functional, method of assessing communities is by the use of guilds, grouping organisms by their exploitation of similar environmental resources in a similar way (Root 1967, Hawkins and MacMahon 1989). This resource-centred method of studying communities allows ecological assessment of them without the full identification of all individuals captured, which is often impossible. The guild concept has three main uses: (1) to study inter-specific competition, the members of a guild competing for the same food resource: (2) to simplify the complex nature of communities: (3) as a natural ecological unit (Hawkins and MacMahon 1989). However guilds are not representative of real levels of organisation within nature. Key studies using the guild method have found proportional guild structure staying constant in habitats even when species composition varied (Moran and Southwood 1982), which ensures that deviations from these normal patterns due to management activity are easily spotted. However definition of the ‘resource’ used and the ‘similar manner’ in which it is
used has to be considered with care. The species must also be occurring at the same place
and time; if not guild association is not guaranteed.

Invertebrates are useful in assessing the effects of environmental variation within
communities. Arthropods have been used in many studies assessing biodiversity levels
dominance in species, numbers and biomass in terrestrial ecosystems and responses to
small changes in environmental conditions such as habitat disturbance and climate
change make them useful in measuring effects of environmental or anthropogenic change
(Kremen et al. 1993). Insects are highly abundant and found in practically all habitats on
the planet. To date 1.7 x 10^6 organisms have been described 56% of which are insects,
around 950 000 species (Speight et al. 1999) and this diversity is increased as new
species are found in underinvestigated but highly biologically rich areas such as tropical
forests. This ubiquity throughout environmental systems highlights both the importance
of insects as a key aspect of biological communities with species performing many varied
functional roles in ecosystems (Speight et al. 1999) and the need for detailed study of the
effects of environmental changes upon them.

One important functional role performed by invertebrates is that of nutrient cycling
within soil systems (Wallwork 1970, Wiegert et al. 1970, Wild 1993), a similar function
having more recently been suggested within the forest canopy system (Schowalter et al.
1981, Lowman 1997). Complex communities of epiphytes and invertebrates have been
found to develop on branches of old growth forest trees both in tropical and temperate
regions (Coxson and Nadkarni 1995, Winchester and Ring 1996, Winchester 1997b) acting as a canopy soil system independent of that of the forest floor. Nutrient cycling from the canopy soil to the tree either occurs directly via canopy roots growing into the epiphyte mats or via nutrient leaching to the forest floor below where it is absorbed by the tree’s main root system (Coxson and Nadkarni 1995). Loss of these systems due to environmental disturbance either natural or anthropogenic can result in severe disruption to the nutrient cycling in forest systems, reducing tree performance and general habitat quality (Schowalter et al. 1981). Insects are therefore performing vital roles within many habitats and are easily used as habitat quality indicators.

These high invertebrate densities and diversities in small areas, highlighted by findings such as the low similarity between invertebrate communities just 10-15 metres apart (Niemela et al. 1996), necessitates maximum use of all available resources within a habitat. This results in a huge variety of lifestyles amongst the invertebrates, both in terms of the types of microhabitats they inhabit and the food sources they utilise. Because they are so small invertebrates can occupy many microhabitats, and so it is that Collembola and Acarina canopy communities have been found to inhabit very different lichen microhabitats on bark surfaces. Collembola prefer lichens with open growth forms while mites prefer crust-like growth forms on the bark (Andre 1985), indeed specific Collembola and Acarina species associate with specific lichen species. Leaf surface characteristics also greatly affect small invertebrates with Acarina abundance and diversity responding to seasonal variations in leaf structure, which particularly affects fungivorous and predatory species, because the leaf structure affects fungus growth and
the hunting environment for the mites (Walter and O'Dowd 1995). Similar levels of
diversification have occurred in feeding habitats within canopies. Invertebrate
communities within canopies are extremely diverse (Southwood et al. 1982a, Erwin
1997) with species feeding on many different species of plants and animals reducing
intra-species competition.

All these factors associated with insects allow the collection of diverse and abundant
biological samples from relatively small areas thereby reducing sampling cost and effort.
The comprehensive samples enable the effects of a single environmental factor, such as
forest edge proximity, to be established for many different invertebrates with varying
lifestyles and food requirements. Insects in the UK are particularly useful for assessing
the effects of environment on communities as their taxonomy and biological functions are
relatively well known compared to those of tropical habitats where little is known about
the species present. This knowledge of the biology of the invertebrates in the UK also
makes classification into guilds easier allowing assessment of environmental factors on
the functional aspects of the forest habitat. Canopy invertebrate communities particularly
were selected for the present research as they are a diverse community in many forest
types (Nadkarni 1994), and are a relatively discrete sampling unit, the canopy being more
or less physically separate from other areas of the forest system, making the definition of
community more specific (see below).
The forest system and more particularly the canopy are a stable and long-term habitat useful in the analysis of the effects of habitat fragmentation on biological systems. Fragmentation has been an increasing pressure on natural habitats within recent years, with decreasing patch sizes and increasing distance between patches due to human activity such as forest clearance (Lovejoy et al. 1986, Andren and Angelstam 1988, Chen et al. 1993, Baldi and Kisbenedek 1994, Camargo and Kapos 1995, Peltonen et al. 1997).

One of the most important effects of fragmentation is the isolation of the habitat patches in a matrix of alternative habitat, leading to highly contrasting boundaries between the two habitat types. These boundaries result in various effects on the abiotic and biotic conditions at the edges of the two habitats termed edge-effects. Increased temperatures and decreased humidities at the edges of forest habitat are a result of increased exposure leading to changes in the suitability of the edge habitat for flora and fauna. If original habitat patches are too small or narrow and edge-effect depths are substantial, i.e. habitat suitability is reduced for many metres into the habitat, patches may be unable to support what are termed core conditions, those of the habitat not influenced by the edge-effect. If core habitat is missing, species particularly associated with that habitat may be absent leading to reduced biodiversity within the area. Information on the depths of edge-effects and the species particularly affected by their presence enables the assessment of suitable patch sizes required to support both edge and core habitat therefore maximising species diversity and reducing the detrimental effects of fragmentation.

This research has a number of aims, attempting to provide a thorough assessment of the effects of edge proximity on the canopy communities of conifer plantations in the UK.
and predictions about the effects of forest management on the resulting edge and core communities. Firstly, more extensive details on the depths of edge-effects in the canopy communities are required beyond that of 50 metres previously studied (Ozanne 1991). This will show whether invertebrates respond to edge proximity to greater depths than 50 metres in conifer canopies, such responses having been reported in other habitats for many organisms including invertebrates (Laurance 1991, Chen et al. 1992, Chen et al. 1995).

Secondly, replicate transects of regularly spaced samples will provide suitable data to enable the clear definition of edge-effect depths by visual assessment and techniques such as squared and relative euclidean distances (Chapter 4). Techniques including squared and relative euclidean distances (S/REDs) have recently been applied to landscape ecology to define the point of transition between habitat types, and have been shown to be useful at the landscape scale (Brunt and Conley 1990, Turner et al. 1991, Johnston et al. 1992). However their use in defining relatively fine scale complex edges along short transects is limited (Brunt and Conley 1990). Squared and relative euclidean distances fail to detect edges when habitat heterogeneity is high compared to the peak produced by the patch edge (Brunt and Conley 1990, Turner et al. 1991), the background variance masking edge variance. As inter-sample variance is high for invertebrate data, particularly density data, the S/RED technique may prove to be of limited use here. The present research will assess its usefulness with small-scale field data and its relative accuracy in comparison to the visual assessment of edge-effect depths.
The defined edge-effect depths from S/REDs and visual assessment will then be applied
to the core-area model (Laurance and Yensen 1991), testing the models efficacy with
field data (Chapter 5). This model was developed from the concept of the species area
relationship, where increasing patch area results in increased species richness, and
attempts to calculate the proportion of habitat patches under core conditions, a more
accurate reflection of pristine habitat patch size than total area (Temple 1986). By using
patch area, perimeter length, patch shape index (Patton 1975) and the edge-effect depth,
the quantity of affected area, which is higher for any given patch size when the shape
index is higher, is deducted from total patch area. This will result in information on the
proportions of each of the research patches under edge and core conditions and therefore
the likely quantities of suitable habitat available for certain invertebrate species. The
model can be further used to assess the affects of proposed edge management on
plantation patches. A number of researchers have highlighted the benefits of sculpturing
plantation edges, by cutting away areas of trees, for a number of invertebrate species
(Greatorex-Davies 1991). However this increase in edge habitat may be beneficial to
some species but could seriously affect the quantity of core habitat available to other, less
apparent, invertebrate species. Applying proposed management to maps of the patches
and re-calculating patch size and perimeter length allows the re-calculation of the
proportions of edge and core habitat using the core-area model, highlighting the actual
changes in quantity of edge and core habitat and the potential knock-on affects to
invertebrate species.
Finally the collection and identification of invertebrates to order, family and where possible species, enabled edge-effects to be calculated not only for invertebrate densities but also species richness, diversity and guild structure. These aspects of the community are likely to respond in different ways to the proximity of edges. Guild structure potentially remaining constant between habitat areas, a constant guild proportion being reported between trees in temperate and tropical forests (Moran and Southwood 1982), but individual species particularly woodland specialists being affected by edge proximity (Ozanne et al. 1997, Peltonen et al. 1997).

The general plan of the study centred upon the effects of edge proximity on the canopy communities in two UK tree species. When investigating a faunal community the community boundaries need to be established, to fulfil the concept of a community being an assemblage of species populations occurring together in space and time. Although the definition of a boundary in communities is artificial, it is necessary to allow analysis and comment on the community to be made. A starting point for defining a community is all those invertebrates utilising a similar habitat either as a food source or a hunting or reproduction site. Therefore all those invertebrates utilising the canopy habitat are considered a community for the purpose of this research.

Discrete canopy communities have been recorded in temperate Picea sitchensis forests, with low percentage species similarity of oribatid mites and Staphylinidae beetles between the canopy and ground (Winchester 1997a and b). More mobile predatory and tourist species show overlap between the canopy and understory communities, with some
species of parasitic wasps (Hymenoptera) actively selecting to hunt in the upper canopy whilst others hunt in both the understory and canopy (Janzen and Gauld 1997). The canopy communities sampled here are likely to represent a similarly discrete faunal unit, apart from a number of tourist species, which do not utilise the canopy habitat itself and some movement of Collembola (Lambert 1970, Bowden 1976, Fjellberg 1992, Hopkin 1997, Prinzing 1997) and Coleoptera (Hammond et al. 1997, Winchester 1997a) from the ground to the tree canopy. The canopy habitat also provides a diverse invertebrate community (Nadkarni 1994), having at least equal if not greater diversity and abundance than the forest floor (Erwin 1982), although the temperate canopy may not support the bulk of forest insect diversity as it does in tropical forests (Preisser et al. 1998). Winchester (1997b) reported higher numbers of Acarina species in the canopy of *Picea sitchensis* trees than on the forest ground or in adjacent clear-fell sites, whilst Stork and Blackburn (1993) found similar abundances, body size and biomass of arthropods between five habitats (canopy, tree trunk, low herb layer, leaf litter and soil) in a rain forest. Studying a diverse community such as that found in the canopy enables the effects of edge proximity on many diverse species of invertebrates to be established.

Conifer plantations were selected over deciduous forests to act as model systems, with the simplified monoculture structure reducing variation in edge-effects and core area size due to habitat heterogeneity, as seen in mixed tree forests which show increased fragmentation due to internal heterogeneity (Bradshaw 1992, Andren 1994). By reducing variation due to internal patch heterogeneity the affects of edge proximity alone can be concentrated on rather than any variations in faunal structure due to habitat heterogeneity.
This concentration on a simple system provides useful information on patterns of edge-effects in invertebrate communities and specific information relevant to plantation forestry and the maximisation of invertebrate species diversity within the habitat. However the use of plantations limits the ability to extrapolate the information to other more complex forest systems but may highlight the position of edge-effects which can be used to direct future research in more complex systems.

Previous research in conifer plantations has centred on economically important invertebrate species, those that harm the timber crop, species such as *Hylobius abietis*, *Ips typographus* and *Elatobium abietinum* having been extensively studied along with their natural enemies under outbreak conditions (Speight and Wainhouse 1989). However a very few studies have investigated the whole UK conifer canopy invertebrate community. One study by Ozanne (1991) established baseline data for canopy invertebrates in four UK conifer species with reference to tree age, patch size, fertiliser application and edge-effects. The present research extends the information on canopy invertebrate communities with specific reference to the effects of edge proximity.

The selection of conifer plantations is important as they are an increasingly dominant forest habitat in the UK making them a key research issue, with the bulk of the increase in forest cover in the UK over the last one hundred years being introduced coniferous species (Peterken 1996). Invertebrate species are extending their ranges into the large areas of introduced conifers, including herbivorous species in general (Southwood 1961, Claridge and Evans 1990) and lepidopteran species in particular (Fraser and Lawton
1994), making them an increasingly important habitat within the UK not just for pest species but a more complete invertebrate community.

As well as acting as a simplified clearly defined system with high invertebrate numbers, plantation forests have the benefit of being transected by many tracks used for timber extraction, which fragment the forests into smaller patches. These tracks provide a system of almost identical edges in the forest running in all compass directions allowing replication of transects from similar edges. Forest tracks are at least a total of 10 metres wide with compacted earth tracks edged by grass swaths. This width of canopy gap has been shown to be enough to induce edge-effects in faunal communities, for example Carabid beetle behaviour was affected by roads as narrow as 3 metres, with individuals rarely crossing over the barrier resulting in isolated communities on either side of the roads (Mader 1984), while plant and forest bird communities have shown both positive and negative effects to narrow (15-80 metre wide) power-line corridors passing through forest areas (Kroodsma 1982, Luken et al. 1992). Forest tracks are also permanent edges, which have been present throughout the lifetime of the trees and therefore result in stable edge-effects, rather than the more rapid edge-effects, which develop after forest clearance (Lovejoy et al. 1986). These features therefore provide a clear and easily definable edge habitat from which to measure effects on canopy invertebrate communities.

Forest areas were selected which provided the largest possible patch sizes for the two conifer species, these were the North York Moors for Pinus sylvestris and Kielder Forest Northumberland for Picea sitchensis. Maximising patch area of the two species ensured
that long transects, at least 100 metres, could be established allowing definition of edge-effect depths beyond the 50 metres previously studied in the UK (Ozanne 1991). Trees were also selected of a similar height, age, planting regime, yield class and growth form, this ensured that coverage by the sample technique was complete and that differences in the trees’ physiology and structure were minimised resulting in a relatively stable invertebrate community. Significant variation in the trees’ age, height or treatment under plantation conditions will lead to differences in the invertebrate community. Ozanne (1991) reported variation in abundance of Collembola and Trichoptera between 25 year old and 10-15 year old conifer species, showing the effects of tree age on aspects of the invertebrate community. Also reported were higher abundances of insects on conifers under higher fertiliser application regimes (Ozanne 1991), showing the potential effect of management on invertebrate communities. Reducing these variations between forest patches ensures that any changes in invertebrate communities found are likely to be due to edge proximity rather than any other feature of the trees.

Selection of two tree species, the native *Pinus sylvestris* and the recently introduced but now widely planted *Picea sitchensis*, allowed investigation into the effects upon the canopy invertebrate community of nativeness, length of time in the flora and the total area of planting. Both length of time in the flora and the area of cover have been shown to have an effect on the invertebrate communities associated with plants (Southwood 1961, Claridge and Wilson 1978, Southwood et al. 1982a, Kennedy and Southwood 1984, Claridge and Evans 1990, Denno and Roderick 1991, Simandl 1993). Native species support a more species-rich invertebrate community than introduced ones,
particularly for those invertebrates closely associated with the plant (herbivore/phytophages), the species having had more time to evolve to the plants physiology (Southwood et al. 1982a, Claridge and Evans 1990). Area or recent abundance of a plant also has an effect on the number of species associated with it (Claridge and Wilson 1978, Kennedy and Southwood 1984, Denno and Roderick 1991), a species highly abundant in the landscape, such as *Picea sitchensis* will be encountered frequently by invertebrates resulting in development of associations between the two species. Detailed comparisons of the invertebrate communities in the two tree species are reported in Chapter 5.

When exploring the effects of edge proximity on the canopy invertebrate community consideration needs to be given to the underlying factors affecting the invertebrate community. Many factors have been proposed as being causative in the development of edge-effects in the fauna and flora at forest edges most centering on abiotic conditions (Chapter 3). Alterations in the abiotic conditions at the exposed edges of plantations result in changes in the microclimate *per se* in those regions, and changes in the flora both physiologically and structurally (Lovejoy et al. 1986. Williams-Linera 1990, Chen et al. 1992, Brothers 1993, Hansen et al. 1993), which have knock-on affects on the fauna. Temperature and light levels have been found to be increased at the edges of plantations whilst relative humidity and water pressure deficit are reduced (Raynor 1971, Williams-Linera 1990, Matlack 1993, Young and Mitchell 1994, Ozanne et al. 1997), with opposite values in core regions. Along with the exact distance from plantation edge of the samples, temperature (°C) and relative humidity (%) were recorded at set distances
from the edge. This allowed the calculation of edge-effect depths, the assessment of their relation to the invertebrate edge-effects, and provided base line data on the pattern of causative factors and the edge-effects reported in the canopy invertebrate community.

The data collected here extends the study of the effects of edge proximity on UK plantation forest invertebrate communities to a greater depth within the plantation patches, probing whether similar and more extensive edge-effect depths occur in these habitats as are seen in other forests in the world (Laurance 1991, Chen et al. 1992, Chen et al. 1995). The data also assesses the usefulness of S/REDs in defining the point of transition between habitat types and the core-area models ability (Laurance and Yensen 1991), when using field data, to predict likely effects of management strategies on the quantities of edge and core habitat and their respective invertebrate communities.

2.1 Introduction.

There are many techniques for ecological sampling but none that is appropriate for every species or habitat; care has therefore to be taken in method selection, as it is critical to answering the question under investigation. Issues of interest in the ecological study of organisms include their habitat requirements, population abundance, distribution and role in the habitat (Southwood 1978, Begon et al. 1990). Assessment of the reasons for a species' increase or decline, the effects of habitat management on species or communities, and the pattern of community structure and function are also of interest. Varying methods of data collection are necessary to explore these questions; the sampling programme must be designed with the target community in mind taking into account among other things their temporal and spatial scale.

This research explores conifer canopy invertebrate communities and their responses to edge proximity and plantation tree species. Therefore, a sampling protocol appropriate for invertebrates, the conifer canopy and the factor of distance from edge was selected. The sampling had to be performed at the appropriate time of year and scale to collect the maximum number of invertebrates, and the specific sampling method needed to be reliable and efficient at removing invertebrates from the conifer canopy. Disturbance of the habitat was kept to a minimum, as were field costs, by selecting a sampling regime that provided quick and relatively cheap samples. To ensure adequate replication without excessive numbers of invertebrates, which would hugely increase sorting and
identification effort, sub-sampling was performed. Sub-samples, are the collection of small randomly placed samples from a habitat rather than the sampling of the whole habitat. These samples are considered to accurately reflect the whole population, with patterns seen within the sub-samples assumed to occur in the whole population.

Detailed consideration had to be given to the temporal scale of the sampling regime as invertebrate abundances and behaviour vary over time, both at the diurnal, seasonal and annual scale (Wolda 1979, Wolda 1983, Lowman 1985, Speight and Wainhouse 1989, Abbott et al. 1992, Gaston and McArdle 1993). As the response of invertebrates to edges occurs throughout the year, due to constant edge presence, sampling could occur at any time of the year. However as seasonal variations occur in invertebrate populations, particularly in temperate areas, collection was carried out between mid-August and early September (Table 2.1), the late summer when food sources of many invertebrates are plentiful, this reduced within year seasonal variation but left yearly variation in the data. Further limitations on sample timing were enforced by the sampling technique being more efficient in the early mornings (Stork and Hammond 1997).

An appropriate sampling scale was selected ensuring suitable data for assessing edge-effects. Gathering samples at the whole forest scale, taking samples every 50 metres from the main forest edge would have been inappropriate, as invertebrates respond to small tracks and gaps within the forest. So edge response needed to be explored from the invertebrates' scale, therefore samples were collected from the canopy of individual trees at set distances from small apparent edges in the forest habitat.
Table 2.1. Site and plantation details for all *Pinus sylvestris* and *Picea sitchensis* sample sites.

<table>
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<th>Factor</th>
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<th>NY 2</th>
<th>NY 3</th>
<th>K 1</th>
<th>K 2</th>
<th>K 3</th>
<th>K 4</th>
<th>KE</th>
<th>KC</th>
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<td><em>Pinus sylvestris</em></td>
<td><em>Pinus sylvestris</em></td>
<td><em>Picea sitchensis</em></td>
<td><em>Picea sitchensis</em></td>
<td><em>Picea sitchensis</em></td>
<td><em>Picea sitchensis</em></td>
<td><em>Picea sitchensis</em></td>
<td><em>Picea sitchensis</em></td>
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<td>9.2</td>
<td>12.5</td>
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<td>54.5</td>
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<td>10-12</td>
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<td>55° 15' / 2° 40' W</td>
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<td>03.09.96</td>
<td>03.09.96</td>
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</tr>
</tbody>
</table>

Sample codes: NY = North Yorkshire, K = Kielder forest, Northumberland, KE = Kielder forest, edge samples, KC = Kielder forest, core samples.
The species under investigation alters the sampling technique required; here as complete a
cross section of the canopy invertebrate community as possible was required. Good
biological knowledge of the species to be investigated is necessary so that appropriate
sampling techniques are selected, or the limitations of the sampling techniques for that
species are known. The use of pitfall traps in an investigation of sedentary ground species
would be inappropriate as the technique is biased towards the collection of active species
(Southwood 1978). In the same way for bark beetles (Scolytidae) which spend most of
their life cycle underneath the bark of trees chemical knockdown methods will fail and
bark removal or emergence traps would be a more appropriate sampling technique.
Despite a number of limitations, discussed in full below, chemical knockdown was
selected for this research, achieving high sample captures of most canopy invertebrates
(Ozanne 1991).

Different habitats present particular problems, which can affect the reliability and efficacy
of sampling methods leading to unrepresentative sampling of the community. When
sampling invertebrates the structure of the habitat is of particular importance due to the
close association of invertebrates and their surrounding habitat. Grasslands and forests
provide different and specific problems for invertebrate capture, the low dense vegetation
of grassland provides considerable cover for them, particularly those occurring on the soil
surface. Different techniques would be required to sample those invertebrates on the grass
(sweep netting) to those occurring on the soil surface below (pitfall trapping).

In the case of forest canopies particular structural problems are encountered when
attempting to sample the whole invertebrate community, desirable for the present
research. There is a general problem with accessibility into the canopy; access techniques introduce human disturbance into the habitat. Any mobile species are likely to have left the target area by the time sampling is performed, leading to an underestimation of their presence in the habitat. Majer and Recher (1988) recorded particularly low abundances of mobile invertebrate species in eucalyptus when samples were collected by branch clipping compared to chemical knockdown, the physical activity of clipping was thought to disturb the invertebrates. Forest canopies also provide a cross section of microhabitats for invertebrates, which require different methods to sample them, those organisms living in or on the bark being less accessible than those on the leaves. Particular problems associated with the sampling methods considered for this research will be discussed later in the chapter.

An appropriate habitat needs to be selected to answer the research question, here, the effects of forest edges on invertebrates. Conifers under plantation conditions were selected because unlike native deciduous forest, they provide a simplified habitat, which increases the chance of finding clearly defined edge-effects. Plantation conifers in the UK support a relatively simple invertebrate community for study (Ozanne 1996), when compared to native deciduous species (Claridge and Evans 1990), as well as having a simplified canopy structure and organised planting regime. The planting of coniferous species in relatively large and angular patches transected by access roads for timber extraction also ensures sharply defined edges between canopy and tracks, from which sampling transects can be extended. In general plantations cover 85% of a forest area, with the road and track system accounting for 8% (Peterken 1996). Since 1960 the area of conifer plantations has exceeded the area of native deciduous forest in Britain (Peterken 1996), making it an
important and ever expanding habitat requiring extensive research.

2.2 Tree Species.

Two conifer species were used during the pilot and main study of arboreal invertebrate communities, these were

*Pinus sylvestris* Linnaeus. Scots pine

*Picea sitchensis* (Bongard) Carriere. Sitka spruce

Scots pine and Sitka spruce were selected for the length of time they have spent in the British flora, and their use as plantation species.

*Pinus sylvestris* is considered to be the only native conifer species in the UK, having been present in the flora since the last glaciation (Rackham 1980). Naturally found in the Highlands of Scotland and northern England, *P. sylvestris* has been increasingly planted in south eastern England in recent years, particularly in Thetford Chase on the borders of Norfolk and Suffolk, and the New Forest in Hampshire (Mitchell 1985), where it thrives as a timber producing tree in the warm dry conditions. Between 1917 and 1927, *P. sylvestris* was one of the most widely planted conifer species in Britain (Peterken 1996). After this period a shift occurred in the species used for plantation forestry and by 1937-1947 planting of the native *P. sylvestris* was being exceeded by *P. sitchensis* (Peterken 1996).
*Picea sitchensis* is native to a narrow coastal band (80 km wide) along the Pacific Northwest of North America from Alaska to California (Savill and Evans 1986). It was introduced to the UK in 1831 from the Queen Charlotte Islands, British Columbia (Peterken, 1996). The use of *P. sitchensis* in UK plantation forestry has increased rapidly since the 1930s, now making it the most commonly planted conifer in the UK (Evans 1987, Speight and Wainhouse, 1989), accounting for *circa* 60% of all planting in 1980 (Peterken 1996).

This variation in length of time in the British flora is of interest when comparing the invertebrate communities of the tree species. It has been proposed that a more species rich community may be found on native species compared to exotic or introduced species (Southwood *et al.* 1982a). Claridge and Evans (1990) studied the species richness of herbivores on 18 trees occurring in Britain, finding 172 herbivore species on *Pinus* sp. (*P. sylvestris* plus some exotics), whilst *Picea* sp. (*P. abies* and *P. sitchensis*) supported 90 herbivore species. The higher species richness on the native conifer genus (*Pinus*) could be the result of both the increased time the tree species has occurred in the British flora (Kennedy and Southwood 1984), and, as proposed by Claridge and Evans (1990), the taxonomic relatedness of the exotic *Pinus* species to *P. sylvestris*.

Why should the taxonomic relatedness of trees in the flora be of importance to their herbivore load? If an introduced tree is taxonomically related to a species of tree already present in the country’s flora, the introduced species can be expected to gain a herbivore community faster than an introduced exotic that is not related to any of the native flora. This is due to the host expansion of preadapted herbivore species. As discussed below,
this factor may well play a more important role in determining the herbivore load than the area occupied by the newly introduced species (Claridge and Evans 1990).

Whilst area is important when considering the expected number of species found on trees along with the latter’s taxonomic relatedness, the past abundance as well as the recent abundance of the host species in the British flora is key. Southwood's study of 1961 showed a significant relationship between the numbers of insect species present on tree species and the abundance of the host plant in geological time (Claridge and Evans 1990). These data have since been reanalysed in the light of the species-area relationship, with the regression showing present tree abundance having the only significant positive relationship with insect species richness (Claridge and Evans 1990). In 1987 Pinus sp. covered 421,021 hectares, whilst Picea sp. covered 646,847 hectares (Locke 1987), by far the largest area covered by one tree genus in the UK. Despite the larger area covered by P. sitchensis and it’s relatives, it has fewer species associated with it than the species-area relationship would suggest, i.e. it falls below the line of the Log area / Log species regression (Evans 1987). However P. sitchensis has gained more species than would be expected for such a recent introduction into the British flora, which is explained by its rapid increase in planted area and its relatedness to Picea abies (Norway spruce) from which herbivore species have crossed (Evans 1987, Fraser and Lawton 1994).

These variations in the species occupation of the British flora, plantation coverage and taxonomic relatedness allow interesting questions to be asked of the data. The two tree species can be expected to support varying complexities of invertebrate communities, i.e. varying species richness, which may respond to the effects of edge proximity in differing
ways. It is also possible to analyse the communities with reference to the inter-genus nature of the data, exploring the issue of taxonomic relatedness of introduced trees. The gathering of new species level data for these tree species, in particular the increasingly planted *P. sitchensis*, will also provide more information enabling compilation of up to date species lists and more accurate species-area relationship analyses to be performed in the future.

### 2.3 Site Selection.

Collection of edge data on canopy invertebrate communities for both the pilot and subsequent studies required field sites situated within UK conifer plantations. Selection of these sites followed a number of criteria listed below. Site details can be found in Table 2.1.

Sites were plantation edges abutting wide forest tracks, public roads or open moorland. Due to the nature of production forestry, extraction tracks are a common feature within UK forests, creating a network of straight wide gaps transecting the forest, often in a regimented grid system. These tracks are approximately 10 metres wide and result in an abrupt change between habitat types, the forest and grass swaths. Using track edges allowed the selection of edges with differing aspects, an important feature as depth of edge-effect varies with aspect (Geiger 1965, Yallop and Hohenkerk 1991, Chen *et al.* 1993, Young and Mitchell 1994, Chen *et al.* 1995). The deepest edge-effects in the Northern Hemisphere are found in edges with a southerly aspect (Geiger 1965, Yallop and Hohenkerk 1991, Chen *et al.* 1995). These south facing edges are exposed to more
extreme abiotic conditions than other aspects, including higher maximum hours of sunlight (Yallop and Hohenkerk 1991), higher levels of solar heat (Geiger 1965) and increased exposure to prevailing winds (Chen et al. 1995). During the pilot study, sites were selected with differing aspects, allowing comparison of edge-effect depth with aspect. For later seasons fieldwork, southerly aspect alone was selected to provide data on maximum edge-effect depths in UK conifer plantations.

Forest patch area was a minimum of 7 hectares (Table 2.1). Patch area is critical to site selection; areas required had to be large enough to establish 100 metre long transects. These patch sizes ensured that the transects did not extend further than the patch and that any point on the transect was more than 100 metres away from forest edges except the research edge, so no combination of edge-effects were affecting the samples. This distance also ensured that core conditions, predicted from previous literature were reached (Williams-Linera 1990, Young and Mitchell 1994, Ozanne et al. 1997).

The trees were between 24 and 43 years old, depending on species. This age range ensured a specific maximum tree height of 9 to 11 metres. Tree height was limited to ensure full canopy sampling with the canopy mistblower, which has a documented maximum spray distance of some 10 metres (Matthews 1985). Delivery of insecticide to heights beyond this could not be ensured, and if attempted would result in inaccurate sampling of the canopy community, with invertebrates from the upper canopy under represented.

Tree condition, judged by productivity was also standardised. The forest industry
classifies stand productivity with the yield class system; this is a record of the potential maximum average rate of timber volume increment that a given stand can achieve. Yield class is calculated as maximum Mean Annual Increment (MAI) of volume production, including dead trees and thinnings, given in timber volume m$^3$/pa (Hibberd 1991). So a stand with a maximum MAI of 14 m$^3$ per hectare, per year, has a yield class of 14. Yield classes of between 8 and 14 were selected for *P. sylvestris*, an average to good yield class rating for the species in the UK (Hibberd 1991). *Picea sitchensis* plantations were also selected that fell in the average yield class rating, between 12 and 16 for *Picea* in the UK.

Ideally sites should be situated in one location to reduce variation in local climate conditions. However this was impossible due to the preferred growth conditions of the tree species under investigation, each preferring different soil types. Sites that conformed to the above criteria were however located in one regional area, Northeast England, to minimise the effect of regional climatic differences. *Pinus sylvestris* sites were located on the North York moors and the vale of York. The largest *P. sitchensis* patches available in the UK are situated in Kielder Forest, Northumberland and sites were selected from this region. Sites conforming to the criteria were initially located through searches of the Forestry Commission sub-compartment database, conducted by various forest district regional offices. Site maps were then obtained and studied, short listed sites visually inspected and a final selection made.

2.4 Transects.

Transects are one of the most commonly used methods for assessing edge-effect depths
They are used at both the landscape level, establishing gradients between regional soil and vegetation types (Beals 1969, Ludwig and Cornelius 1987, Johnston et al. 1992), and those edge-effects of just a few metres running across the borders of differing vegetation types (Chapter 3). One specific type of transect is the gradient directed transect or gradsect, which is aligned along environmental gradients (i.e. altitude) to assess variation in a given factor (flora or fauna) along that gradient. Gradsects can assess both regional and local gradients, and are particularly useful when exploring edge-effects, the gradsect running along the expected variation from plantation edge.

Care should be taken when considering gradsects, for an assumption is being made as to the main cause of the variation seen in the factor being studied, i.e. is edge proximity the real contributing factor to the edge-effects seen in invertebrates at forest edges, or is there some other, as yet un-established underlying cause? Transect data can also limit analysis used on the data, by providing non randomised sample points. However new methods for transect data analysis have been developed to improve the definition of edge-effects from transect data. These include variations on the split moving window technique (Chapter 3).

Transects were established in a number of forest patches of each conifer species, to ensure invertebrate samples were replicated and no particular patterns distinct to one forest patch were emphasised. Three patches each with a single transect were sampled in one year for *P. sylvestris*; the patches just large enough to support one transect (Table 2.1). For *P. sitchensis*, two large patches were used, one with a single transect, not repeated due to an internal edge, and one with three transects established within it. Multiple transects were possible due to the large size and long edge of this patch, with transects always at least 50...
Transects running perpendicular to forest track edges were established extending a minimum of 100 metres, to encounter core conditions, into the forest patches. Sample points were selected along the length of each transect at distances appropriate to the expected rate of change in the invertebrate community, with edge-effects often being more dramatic over the first 50 metres (Williams-Linera 1990, Young and Mitchell 1994). If inter-sample distances were considerable at the edge, i.e. 20 metres, significant changes occurring between the samples at zero and twenty metres would be missed. Within the first 50 metres of plantation edge inter-sample distance was 5 metres, ensuring detailed data from the area with greatest expected change. Beyond 50 metres inter-sample distance increased to 10 metres, enabling greater transect depth to be achieved without increasing sample number.

Additional edge (0-10m) and core (80-120m) data were collected during the final field season, increasing data on gross differences between the edge and core habitat. Blocks of samples in grids of five were taken in the edge and core areas of *Picea sitchensis* plantations; four replicates were collected giving 20 extra samples in each region. These distances were selected to ensure that the samples were likely to encounter the most extreme differences in the invertebrate community possible within these plantation patches. The very edge samples at 0-10 metres fall within the edge zone of high invertebrate contrast reported in previous research (Helle and Muona 1985, Baldi and Kisbenedek 1994, Bedford and Usher 1994, Ozanne *et al.* 1997), whilst the 80-120 metre samples are at the greatest possible depth from plantation edge in these particular
plantations and are beyond the 50 metre mean edge-effect depth reported by many researchers (Williams-Linera 1990, Young and Mitchell 1994).

2.5 Abiotic sampling.

Abiotic variations are strong driving forces behind community organisation (Dunson and Travis 1991) and behind edge-effects (Lovejoy et al. 1986, Matlack 1993, Young and Mitchell 1994); it is therefore vital to ensure accurate gathering of abiotic data is achieved to relate to the invertebrate data. Temperature (°C) and relative humidity (%) data were collected within the canopy at points corresponding to the invertebrate sampling points. These factors were selected as they have been found to be particularly important to invertebrates (Kidd and Tozer 1985, Larsson 1985, Barnes 1987, Prinzing 1997, Prinzing and Wirtz 1997), and they can be collected with relative ease using an automated data logger.

Ideally abiotic information should be collected on a long-term basis in the given area of study so that diurnal and seasonal variations in climatic factors can be eliminated and the establishment of true abiotic edge-effects achieved. However the collection of abiotic data in this way was impossible due to limited funding, preventing establishment of long term meteorological stations in the forest canopy. Rather, on-the-spot information on abiotic factors at the time of sampling were collected. Temperature and relative humidity readings were taken between 1.5 and 2 metres above the ground adjacent to the sampling
points with a Delta-T (Delta-T Devices Ltd, UK) automated data logger, with a RHA 1
temperature and relative humidity probe set to log readings every minute. Three readings
were taken at each sample point during the drop time, allowing a mean temperature and
humidity reading to be established for each point along the transect line. The data logger
was then transported to the next sampling point and left to calibrate for at least 3 minutes
before the next set of readings were automatically recorded. These readings provided
enough information to determine the presence of gross variations in microclimate with
distance from edge.

2.6 Invertebrate sampling.

A number of sampling techniques for biotic and abiotic factors were used during this
study, to collect appropriate data to answer research questions. The selection of sampling
techniques ensured the collection of samples representative of the canopy invertebrate
community, providing as complete a representation as possible of all invertebrate species
and guilds from all heights in the canopy.

2.6.1 Chemical knockdown.

Chemical knockdown methods, both mistblowing and fogging, have been used for a
number of years as an effective method of invertebrate collection from the canopy habitat.
Early knockdown use in the 1960s centred around pest control but was developed as a
method of ecological sampling, particularly in the forest habitat, by Altenkirch in the mid­
sixties (Paarmann and Kerck 1997). Initial use had limited success due to the poor
knockdown qualities of the chemical used, DDT, which failed to disrupt invertebrates enough to remove them from the canopy. Chemical knockdown became more successful in the late sixties with the development of pyrethrum based insecticides, showing fast knockdown properties (Martin 1966, Gagne and Martin 1968). Research using knockdown collection of forest invertebrates has increased steadily since the seventies, with an array of studies in both tropical (Stork 1987a and b, Erwin 1983, Allison et al. 1993, Kitching et al. 1993, Russell-Smith and Stork 1995, Adis et al. 1997) and temperate regions (Southwood et al. 1982a, Moran and Southwood 1982, Barnard et al. 1986, Ozanne et al. 1997).

Chemical knockdown is more effective than other canopy sampling methods, such as branch clipping or beating and aerial malaise traps, providing high numbers of a representative cross section of the community. Southwood and colleagues (1982b) compared knockdown samples from six British tree species with their respective faunal lists. The knockdown samples reflected the relative species richness of arboreal communities well when compared to the faunal lists (Southwood et al. 1982b). Majer and Recher (1988) compared branch clipping and chemical knockdown sampling in two types of eucalypt forest. The two techniques gave similar relative abundance results for the invertebrates, however chemical knockdown sampled more species. Both techniques showed weaknesses, with chemical knockdown underestimating sessile invertebrates, whilst branch clipping poorly represents large, mobile or cryptic species (Majer and Recher 1988). They concluded that although chemical knockdown is a superior technique, branch clipping or shaking can be used as an alternative when conditions are poor for knockdown and when specific canopy distribution is of interest, as long as relative
abundance rather than species diversity is considered (Majer et al. 1996). However other researchers have suggested that in the more complex canopies of tropical forest no single technique is adequate at sampling the whole invertebrate community and a combination of techniques should be used to achieve maximum community sampling (Basset et al. 1997, Stork and Hammond 1997). The use of chemical knockdown in the simple conifer canopy under investigation here was appropriate to collect the largest proportion of the invertebrate community possible.

Two specific methods of knockdown chemical application are used for ecological sampling of forests, fogging and mistblowing. Fogging is the preferred technique in the tropics, with its greater capacity for dispersing knockdown agent throughout tall canopies. The fogger uses a thermal-energy nozzle through which hot gases pass, derived from the exhaust of a combustion chamber (Matthews 1985). Oil based solutions of pesticides are passed through a restrictor into the exhaust pipe, where the insecticide is vaporised at temperatures around 500°C, forming a 'fog'. This warm pesticide 'fog' disperses throughout the sample area, but can drift beyond the designated area in even light air currents (Matthews 1985, Stork and Hammond 1997), potentially resulting in contamination of additional forest canopy. Adis and workers (1997) reported invertebrate capture of mostly small winged insects in trays 20 metres from the fogged area (Adis et al. 1997). Therefore insecticide concentrations beyond the sample area may not be strong enough to affect larger invertebrates, but could have a significant effect on the smaller aspect of the invertebrate community.

In comparison, mistblowing relies on an air current to create droplets and disperse the
knockdown agent through the sample area. Small droplets of insecticide are added to an airstream, created by a powered fan, these shatter into a mist (30-100μm) which is propelled through the sample space. Air velocity decreases rapidly once the spray leaves the nozzle; sampling distance is therefore restricted by the power of the fan. Vertical distances in the range of 6 to 10 metres can be achieved (Matthews 1985) with a maximum distance of 15 metres. Despite the height restriction, spray direction can be controlled more precisely than fogging, resulting in less site contamination. Air movement affects the method less (Stork and Hammond 1997), although small invertebrates can be lost during the drop time if air movement is great, taking them beyond the sample area (Adis et al. 1997). Both sampling techniques are sensitive to environmental conditions other than air currents, for example dampness disrupts both the movement and efficacy of knockdown chemicals, leading to unevenly distributed dilute solutions around the canopy (Himel and Moore 1969, Smith and Burt 1970, Johnstone 1985, Grafius 1986, Majer et al. 1996, Stork and Hammond 1997). Sampling should therefore be performed under dry still conditions, most usually associated with early mornings. This preference for morning sampling introduces bias into the sampling regime, underestimating the effects of diurnal changes in invertebrate communities.

Low site contamination was preferable for the present study, so the localised application of insecticide by mistblowing technique was selected. Mistblowing has also been used in previous UK based conifer canopy research (Ozanne 1991), so its use in this study ensured that samples were comparable with previous studies. The technique achieved a spray height that was sufficient to collect samples from mid-rotation, 25 to 35 year old conifer trees, at top heights nearing 10 metres.
2.6.2 Mistblowing.

A Hurricane Major mistblower (Cooper-Pegler) was used to disperse Pybuthrin 2/16 (AgrEvo UK Ltd) insecticide within the forest canopy. This mistblower has a compact backpack design making it easy to use in the confined conditions of conifer plantations, it has proven reliability and is capable of Ultra Low Volume (ULV) insecticide application. ULV is the application of chemicals at rates below 20 litres/ha (Johnstone 1985), by the use of a very fine mist of droplets. This mist results in improved penetration of the canopy increasing the likelihood of sampling the whole arboreal community (Johnstone 1985, Matthews 1985, Ozanne 1991). It also results in low chemical use, reducing costs and causing few long-term environmental problems, with canopy invertebrate communities found to recover in as little as three months (Stork and Hammond 1997).

Pybuthrin 2/16, is a fast acting pyrethrin based knockdown chemical especially formulated for ULV spraying. It contains a mixture of natural pyrethrins derived from Chrysanthemum cinerariaefolium, including Pyrethrin I and II, Cinerin I and II, and Jasmolin I and II. These are suspended in refined petroleum (kerosene), with the synergist, piperonyl butoxide (AgrEvo pers. comm.). Pyrethrin based insecticides show short-term effects on the environment, the active ingredients having a half-life of 48 hours in ultra violet (UV) light (AgrEvo pers. comm. 1998, Barlow 1985). Minimising environmental effects is preferable as long lasting effects could affect subsequent sampling regimes due to disruption of the invertebrate community or alteration in plant biochemistry. Pybuthrin 2/16 is highly specific to invertebrates with low mammalian toxicity, however the
chemical has severe effects on aquatic life, so contamination of water bodies must be avoided. Full health and safety guidelines were adhered to whilst handling the chemical including training in the safe use of pesticides and their application, and the use of full body suit, gloves, boots, respirator, face shield and ear defenders whilst spraying.

Pybuthrin 2/16 achieves knockdown by inducing repetitive axon firing in invertebrates, resulting in a loss of co-ordinated movement and attachment to the substrate (Barlow 1985). Knockdown can be rapid, occurring in minutes, although differential rates of absorption through the cuticle depending on species, can extend this time to more than an hour, with invertebrates still falling after one hour post-spray (Ozanne 1991, Adis et al. 1997, Paarmann and Kerck 1997). The longevity of knockdown is enhanced by the introduction of a synergist to the insecticide. Synergists are designed to block the recovery mechanisms of invertebrates ensuring more rapid and long term knockdown in species with good recovery systems or showing pesticide resistance (Ishaaya 1993). Piperonyl butoxide specifically inhibits oxidation of various pyrethroids. Larger species are capable of recovering from a knockdown event, particularly if they have a highly developed detoxification mechanism based on either hydrolytic or oxidative pyrethroid esterase’s (Ishaaya 1993), allowing the collection of living specimens from canopies for investigations into life history strategies. Beetles (Carabidae) collected by Paarmann and Stork (1987) from tropical canopies, recovered within 24 hours of the knockdown event. With an average of 50 to 60% survival of insects after 7 days, when collected with different chemical concentrations (Adis et al. 1997).

Invertebrates knocked down using pyrethrum need to be captured beneath the canopy, and
various methods have been used ranging from plastic or cloth sheets of no fixed area, placed on the ground to specifically designed trays of known area. Drop trays of a standard design developed by the Natural History Museum, London (Brendell 1997) were used in this study. They consist of 1 metre squared funnel shaped trays of silicone coated nylon, supported by a circular collapsible metal frame. At the funnel apex is a threaded rim into which a quarter litre plastic bottle can be attached. The trays are suspended from a three line harness (Brendell 1997, Brendell pers. comm. 1995), which can be attached to a rope system beneath the canopy or clipped directly onto lower branches. The known area of the trays allows a degree of quantification of the samples, receiving the fall out from a metre area column of a known height of canopy. However full quantification is difficult as canopy depth and quantity above the trays can be variable, making comparisons between trees species, which may have different canopy structure, somewhat conjectural.

2.6.3 Sampling protocol.

Drop trays were suspended from lower branches one metre above ground level and approximately 30 centimetres away from the trunk, at fixed distances along a transect running perpendicular to forest edge. This gathering of data at fixed distances from the edge, with regular sampling distance, provided information on invertebrates with distance from edge, enabling evaluation of edge-effects.

Once drop tray location was established plastic bottles containing 70% ethanol and an identification label were attached to the trays. The canopy above each tray was sprayed for
a period of 30 seconds, applying 120 ml of Pybuthrin 2/16 to each sample area, at a flow rate of 240 ml/min, a flow rate from this mistblower that achieves even coverage in the upper canopies of conifers (Ozanne 1991). A drop time of 2 hours for the invertebrates to enter the trays was allowed then they were gently brushed into the collection bottles, which were removed and sealed.

During the two-hour drop time abiotic data, temperature (°C) and relative humidity (%) were collected. Temperature and relative humidity readings were taken at an average height of 1.5 metres above ground level, equal to the height of the drop trays. The data logger probes were situated adjacent to the sampling tray and allowed to calibrate for at least 3 minutes. Three readings were then taken at one minute intervals at each sampling point being automatically recorded by the data logger, before being moved on to the next position.

Invertebrates were separated by hand from any plant material in the sample, counted, identified to order using Tilling (1987) and placed in fresh 70% ethanol. Identification to species of the Araneae was by Mr. C. Hambler, University of Oxford, the Acarina by Dr. A. Baker, Natural History Museum London and assistance with Collembola came from Dr. P. Shaw, Roehampton Institute London. Further assistance was given by Dr. C.M.P. Ozanne, Roehampton Institute London. All other identification to family, genus and species where applicable was performed by the author, the Coleoptera using Crowson (1956) and Unwin (1984), and Coccinellidae, Pope (1953). Table 2.2 shows the families and species identified in *Pinus sylvestris* and *Picea sitchensis*. 
Table 2.2. List of taxa identified in mist blowing samples from the canopies of *Pinus sylvestris* and *Picea sitchensis* in the UK.

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Species</th>
<th>Tree Species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Acarina</strong></td>
<td>Mesostigmata</td>
<td><em>Pergamasus</em> sp.</td>
<td><em>P.sit</em></td>
</tr>
<tr>
<td></td>
<td>Oribatida</td>
<td><em>Belba</em> sp.</td>
<td><em>P.sit</em></td>
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<td></td>
<td></td>
<td><em>Camisia</em> sp.</td>
<td><em>P.sit / P.syl</em></td>
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<td></td>
<td></td>
<td><em>Carabodes</em> sp.</td>
<td><em>P.syl</em></td>
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<tr>
<td></td>
<td></td>
<td><em>Cepheus</em> sp.</td>
<td><em>P.syl</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Ceratoppia</em> sp.</td>
<td><em>P.sit / P.syl</em></td>
</tr>
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<td></td>
<td></td>
<td><em>Chamobates</em> sp.</td>
<td><em>P.sit / P.syl</em></td>
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<td></td>
<td></td>
<td><em>Cymbaeremaeus</em> sp.</td>
<td><em>P.syl</em></td>
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<td></td>
<td></td>
<td><em>Platynothrus</em> sp.</td>
<td><em>P.sit</em></td>
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<tr>
<td><strong>Prostigmata</strong></td>
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<td><em>Anystis</em> sp.</td>
<td><em>P.sit / P.syl</em></td>
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<td></td>
<td></td>
<td><em>Bedella</em> sp.</td>
<td><em>P.sit / P.syl</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Leptus</em> sp.</td>
<td><em>P.sit / P.syl</em></td>
</tr>
<tr>
<td><strong>Araneae</strong></td>
<td>Araneidae</td>
<td><em>Araneus diadematus</em></td>
<td><em>P.syl</em></td>
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<tr>
<td></td>
<td></td>
<td><em>Araniella</em> sp.</td>
<td><em>P.syl</em></td>
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<td><em>Atea</em> sp.</td>
<td><em>P.syl</em></td>
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<td><em>Cyclosa conica</em></td>
<td><em>P.syl</em></td>
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<td><em>Gibbaranea gibbosa</em></td>
<td><em>P.syl</em></td>
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<td></td>
<td><em>Nuctenea umbratica</em></td>
<td><em>P.syl</em></td>
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<td>Adalia 10-punctata var.</td>
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2.6.4 Invertebrate data handling.

The invertebrate data were analysed in a number of ways within the chapters of this thesis, answering specific research questions; these methods will be detailed here to prevent repetition in the methodologies of individual chapters. Alterations to these methods or specific techniques will be discussed in detail in the appropriate section.

Due to standardisation problems of invertebrate data from canopy studies, a result of variations in the quantity of canopy material above the drop trays, invertebrate mean density data per m² ground area (the size of the collection trays) was used over total abundances, maximising standardisation of the data. Invertebrate densities were calculated either as total invertebrate density per m², or for individual taxa per m². These density calculations were either used in their raw state with each figure being plotted on a graph against distance from plantation edge thus exploring effects of edge proximity on invertebrate densities (Chapter 3), or the density data were used to explore gross differences in invertebrate densities between edge and core areas, by comparing mean edge (0-15m) densities of total invertebrates and invertebrate taxa, with mean core (80-120m) densities (Chapter 3). Therefore invertebrate density data at the sample, group of sample, transect or tree species level were comparable, allowing exploration of invertebrate responses to edge proximity and tree species at a number of scales.

Further to invertebrate density data, the species composition of the invertebrate community was of interest and this was explored in a number of ways, from the comparison of invertebrate species lists, to the analysis of species richness and species
diversity. As mentioned, invertebrates were in general taken to order, four of which were classified further. These were the Acarina, Araneae, Coleoptera and Collembola classified where possible to species. The Coleoptera order was taken as far as family with just the diverse Coccinellidae family, an important predatory species in conifers, identified to species. These orders were selected as they have previously been shown to be important in the invertebrate canopy community (Gunnarsson 1988, Walter and O'Dowd 1995, Winchester 1997a and b, Walter and Behan-Pelletier 1999) and taxonomic help was available for identification. It was therefore possible to make comparisons across the data set at the order level and to make more detailed comparisons of these four key orders.

Straight comparisons of the species encountered (species lists) were particularly useful when considering differences between the two tree species (Chapter 5) highlighting key differences in the invertebrate communities of the two habitats. Other questions of interest included the response of invertebrate richness and diversity to edge proximity and tree species. Species richness is a method of exploring the number of species or taxon in a given sample unit. The number of species can only be compared if they are based on the same sample size, as species capture increases with sampling effort (either time or number of samples) up to a finite number, therefore analysis has to be performed between the same number of samples and converted to a mean value.

Invertebrate richness could be calculated for the whole invertebrate community or for family/species richness for the Acarina, Araneae, Coleoptera or Collembola in any group of samples or between transect data. Richness was calculated by dividing the sum of species in each of the samples by the number of samples, giving a mean richness value.
Gross responses of invertebrate richness to edge proximity were again explored by comparing edge and core samples (Chapter 3), with general trends in richness from plantation edge being plotted on graphs, using replicate transects to provide mean data (Chapter 3). Invertebrate richness differences between the two tree species were compared at the community and order level, to explore whether tree species and its time in the flora affected invertebrate richness (Chapter 5).

Species richness on its own however fails to tell the complete story when it comes to the structure of the invertebrate community. Although the technique is useful it does not account for the rarity or abundance of different species. Two communities each with eight species would be considered the same when comparing richness, however one community might have equal abundances of a number of common species whilst the other may only contain a number of rare species with low abundances. So, while species richness would represent them as the same, the latter might be of more conservation interest due to the presence of rare species. The use of a diversity index takes into account the species richness of a community and the abundance of its component species. However indices have limitations, results being affected by the composition of the community particularly sample size, and the abundance and distribution of the community (Magurran 1988). If inter habitat samples have very different abundance and distribution patterns comparison will not be informative, overestimating these factors rather than variation in diversity itself, therefore comparison was not made between the two tree species. The simple Simpson’s index (Southwood 1978) was used here, the technique making limited, and therefore less
inaccurate assumptions of the data:

\[ C = \sum (N_i / N_t)^2 \]  \hspace{1cm} (2.1)

\( N_i \) = number of individuals of species \( i \)
\( N_t \) = total number of individuals in sample

\((C)\) predicts the probability of the next species sampled being the same as the last species sampled. A low \((C)\) value indicates a community dominated by one species or a community with equal abundance throughout the species present. This is opposite to what intuitively would be expected so the equation result is reversed to the Dominance index \((D)\):

\[ D = 1 / C \]  \hspace{1cm} (2.2)

Now the greater the value of \( D \) the greater the dominance by one species. The value of the index depends on both the species richness and evenness (equitability) of distribution of the abundance amongst the species. Therefore for a given richness \( D \) increases with equitability, and for a given equitability \( D \) increases with richness.

The Simpson’s index is a widely used index, including in previous UK invertebrate canopy research (Ozanne 1991), it shows reasonable discriminatory ability (Magurran 1988) being able to detect relatively small differences between communities, it also shows low sensitivity to sample size. The technique is however biased towards dominance within the community rather than richness. This is more useful in the data set as inter-sample richness variations are high whilst abundance patterns are relatively similar, resulting in
any differences seen in the results not being a reflection of richness alone but more a reflection of some other diversity difference between the communities. Other diversity indices are heavily affected by richness (Magurran 1988) therefore highlighting differences in richness alone and providing little more information than species richness analysis. The diversity index here provides information on the dominance pattern seen within the invertebrate communities; communities with high D values are dominated by one or two species.

2.6.5 Guild classification.

Over and above the species level analysis of the invertebrate community guild analysis was performed on the data. The classification of invertebrates into guilds, which ignores taxonomy, and grouping species by their exploitation of similar environmental resources (Hawkins and MacMahon 1989), allows some form of ecological assessment of communities without the complexity of attempting to classify organisms into their taxonomic levels. It also takes into account that many organisms use similar resources, so the emphasis of the research is more resource centred. The species utilising similar resources may be expected to have considerable levels of overlap in their interactions and therefore considerably to influence the communities they inhabit (Adams 1985).

Ecological analysis of communities beyond the detailed analysis of food webs or one-to-one relationships is desirable, however, a complex description of all the interactions in a community is virtually impossible (Adams 1985). A method which maintains a significant quantity of biological information whilst simplifying the descriptions could be useful, and
the guild is a development along these lines. The technique is however strongly contested, some viewing it as a useful natural unit reflecting resource use in the habitat, others considering it a non-existent construct of ecologists, oversimplifying ecological interactions and bearing no resemblance to the real world (Hawkins and MacMahon 1989). The usefulness of guilds lies in the stability of the associations. Although the abundance and species composition in a habitat may vary considerably, guild structure is more stable and predictable, guilds maintaining their abundance at or near the carrying capacity despite the fluctuations of individuals within the guild (Hawkins and MacMahon 1989). Moran and Southwood (1982) reported in their classic guild study, that arboreal invertebrates in various tree species in both Britain and South Africa had similar proportions of predatory species and also a constant proportion of phytophagous species on different broad-leaved trees. This means a similar percentage of each canopy invertebrate community irrespective of tree species is made up of the phytophagous or predatory guilds, supporting the idea of a stable trophic structure (Moran and Southwood 1982).

Guilds were used in the present research to assess the responses to edge proximity at the ecological function scale, changes in guild proportion potentially suggesting an alteration in resource availability in the canopy. Their use also allowed comparison with previous UK plantation canopy work (Ozanne 1991), allowing assessment of the constancy of guild proportions in canopy invertebrate communities in these tree species. Guild classification (Table 2.3) was adapted from Moran and Southwood (1982) and Simandl (1993) both of which give detailed listings of UK canopy invertebrates and their classification into guilds. Six relatively simple guild groupings (Table 2.3) were used
Table 2.3. Guild assignment for invertebrate taxa adapted from Moran and Southwood (1982) and Simandl (1983).

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<tr>
<td>Tricoptera</td>
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</tbody>
</table>
because identification to order inhibited the construction of very detailed groupings as the functional role of some of the orders would be mixed, and where this occurred the most dominant functional role of the order was used. Once guilds had been constructed they were analysed in a similar method to the species data, with comparisons of guild densities, percentages and richness being made between various samples.

A further more functional way of assessing invertebrate communities is by exploring predator/prey ratios and therefore the predatory pressure on invertebrates. Predator/prey ratios are altered by edge proximity (Ozanne et al. 1997), with higher predator/prey ratios in edge habitats, meaning more predators per prey item in this zone. Ideally when assessing predator/prey ratios the ratio between a prey organism and its specific predators will be established however this requires detailed knowledge of predatory species preferences for prey items which is often impossible to establish in the wild. Predator/prey ratios can be more generally established by grouping all predatory and parasitic organisms together (Table 2.3), and establishing their ratio to all other invertebrates captured, i.e. all potential prey items. This technique was used in the present research and mean predator/prey ratios compared against distance from edge and between tree species.
Chapter 3. Edge-Effects.

3.1 Introduction.

Fragmentation of forested areas by both sustainable and unsustainable forest management activities, both historically and in the present day, is widespread throughout the world. In the UK, forest cover has reduced considerably from a total woodland cover of 85% of total land area in 3000 BC to just 11% of land area in AD 1992 (Peterken 1996). A recovery from a previous low of just 4% woodland cover in AD 1895, due to overexploitation of the forest resources of the Nation. The recent increase in total forest cover has been associated with an increase in coniferous woodland as a percentage of total woodland cover, with a net increase of 199% in coniferous species in the UK (Warren and Key 1991). In 3000 BC coniferous woodland made up just 15% of total woodland cover (Peterken 1996), being comprised mainly of natural Caledonian pine forests, this had increased to 25% by 1895 and 70% by 1992 (Peterken 1996). The bulk of the increase of total forest cover from 1895 to 1992 has therefore been with the replanting of coniferous species rather than native broadleaved species. Perhaps more importantly this increase has been by planting exotic conifer species, leading to a rapid change in the tree species composition of the United Kingdom. Such a change in composition could reduce the recovery rate of native woodland faunal species in the increasing woodland cover as they attempt to associate with the new tree species, e.g. the saproxylic beetles (Warren and Key 1991). These Coleoptera are in serious decline in the
UK, with high species loss, just a few species increasing in abundance associated with
decaying softwood timber of non-native plantation forests (Warren and Key 1991).

The increase in conifer plantations in the UK has lead to a number of general changes in
the landscape pattern of UK forestry with resulting effects on biotic communities living
within the forest. Plantations are highly managed ecosystems with a regular construction
pattern of plantation patches and extraction roads (Hibberd 1991). Day to day
management differs from that of natural woodland, with thinning, fertiliser application
and clear cutting processes occurring throughout the lifetime of the forest. Two of these
factors are of particular relevance to the present research, clear-felling and the road
system of plantation forests.

Clear-felling and the construction of forest roads develop physical edges in the forest
environment. In the first instance by the sudden and extreme edge creation by clear-
felling activity with trees being exposed to a large expanse of adjoining clearfell, in the
second the long-term development of edges of plantations next to forest tracks, which
although less exposed than clearfells, still provide a strip of open habitat at least 10
metres wide, running through the forest. Both types of edges have many effects on abiotic
conditions, ecological processes and the fauna and flora of the adjacent forest habitat,
resulting in alterations termed edge-effects. Forest edges adjacent to forest tracks are of
particular interest here due to their ubiquity in plantation forestry, and their likelihood of
showing clearly established edge-effects rather than the potentially dramatic and variable
responses of edges to neighbouring clear felling activity which often include windthrow
with the edge slowly encroaching into the forest (Lovejoy et al. 1986), whereas track edges are unmoving and clearly definable.

Changes in microclimate at forest edges have been documented in both tropical and temperate forest systems (Raynor 1971, Lovejoy et al. 1986, Williams-Linera 1990, Chen et al. 1993, Matlack 1993, Young and Mitchell 1994, Camargo and Kapos 1995, Ozanne et al. 1997). Abiotic factors altered include, temperature, relative humidity, gross light levels, photosynthetically active radiation levels (PAR), vapour pressure deficit (VPD) and wind speed. These studies have looked at the relative changes in these factors along transects running from forest edge into the forest habitat, attempting to ascertain where abiotic conditions appear to stabilise, giving rise to what may be considered 'core' conditions. This edge-effect depth is altered by many factors including the abiotic condition under investigation, type of tree species, edge orientation and sharpness of the edge. Studies support an average edge-effect depth of 50 metres for abiotic factors with the most extreme variation occurring over the first 15 metres (Williams-Linera 1990, Young and Mitchell 1994). Research bias towards studying the first 50 metres of forest edges may however account for this average, with edge-effects of up to 240 metres being found in microclimates of old growth Douglas fir forests (Chen et al. 1995).

Abiotic edge-effects may directly or indirectly affect the biotic aspect of the habitat, both plants and animals. Quite extreme responses to forest edge are seen in the plant community (Lovejoy et al. 1986, Laurance 1991, Malcolm 1994, Young and Mitchell 1994) which in turn affects food supply and the habitat conditions of the animals.
inhabiting the area, which either respond in a positive (higher densities or richness at the edge) or negative (lower densities or richness at the edge) way.

Vegetation structures, both understory and canopy, of tropical and temperate forests show varying depths of edge-effects; density, basal area, community structure, tree mortality and growing season are all affected by edge (Lovejoy et al. 1986, Williams-Linera 1990, Laurance 1991, Young and Mitchell 1994, Chen et al. 1995, Scariot 1999). Depths of floristic edge-effects are more variable and of a greater depth than those found for microclimatic factors. Disturbance adapted plants have been found to be unusually abundant within 500 metres of forest edge (Laurance 1991). Different age classes of the same species can also respond differently to edge proximity, western hemlock seedlings (0-10cm) had an edge-effect depth of 137m, whilst taller (31-100 cm) seedlings showed variation for just 16 metres (Chen et al. 1992), both showing increased densities in the edge.

A common response of newly created edges such as those found next to clear fell areas is an increase in tree mortality and windthrow in the edge zone (Williams-Linera 1990, Chen et al. 1992), often resulting in pest outbreaks. However this effect is seen less in the slowly established edges next to plantations roads, where lateral growth of branches tends to occur (Forman and Godron 1986, Lovejoy et al. 1986, Williams-Linera 1990, Chen et al. 1992). This regrowth at the edge results in a flush of young needles and a continual greening of the area increasing potential food supply for the herbivorous element of the animal community.
Faunal edge-effects have been studied for many species including birds, mammals, amphibians and invertebrates (Helle and Muona 1985, Rosenberg and Raphael 1986, Andren and Angelstam 1988, Medley 1993, Andren 1994, Baldi and Kisbenedek 1994, Bedford and Usher 1994, Ozanne et al. 1997, Peltonen et al. 1997). In a similar way to the flora, edge-effects in forest fauna are variable with both positive and negative effects of varying depths, from a few metres to over one hundred metres.

Invertebrate edge-effects have mainly been found for ground and understory communities, with less research on canopy communities (Ozanne et al. 1997). Responses to edge proximity vary greatly with the species under investigation, generalist invertebrates thriving in edge conditions, with specialist forest species retreating into core areas of forest (Peltonen et al. 1997). It is often stated that edges are beneficial in the forest habitat due to the increased species richness and abundance found in some edge habitats, a result of the fusion of two communities (Helle and Muona 1985, Baldi and Kisbenedek 1994, Bedford and Usher 1994). This extension of the open habitat community into the edge zone of the forest may well increase species richness but can potentially increase competition and predation rates there. This would particularly affect sensitive woodland specialist species, which may be unable to out-compete generalist species from the open habitat. However species richness is not increased at all forest edges (Ozanne et al. 1997) and the creation of edges in the forest habitat may be detrimental to a number of species (Ozanne et al. 1997, Peltonen et al. 1997).
In addition to research into invertebrate densities, richness and diversity, studies have examined the effects of edge proximity on the more functional aspects of communities, particularly guilds. The assembly of organisms into functional groups, guilds, is derived from their utilisation of similar environmental resources (Hawkins and MacMahon 1989). Guild structure is thought to be more stable than that of arthropod densities or richness, with guild species composition varying but a relative proportion of the guilds within a community remaining constant (Moran and Southwood 1982, Stork 1987a, Hawkins and MacMahon 1989, Wilson 1989). Research into Norway spruce (Picea abies) canopy arthropod communities reported edge-effects in the predators, herbivores and detritivores, with the predatory and herbivorous guild proportions in the community increasing at the edge with a proportional decrease in the detritivore guild (Ozanne et al. 1997). The higher proportion of herbivores at the edge is likely to be a response to increased food quality and quantity there due to lateral needle flush (Forman and Godron 1986, Lovejoy et al. 1986, Williams-Linera 1990, Chen et al. 1992). The predatory guild following the same pattern, proportionally increasing with the increase in herbivorous prey items in the edge.

A further functional approach to edge-effects is the analysis of predator/prey ratios and how edges affect the balance of the predator/prey relationship. Increased predator/prey ratios have been reported in edge habitat (Ozanne et al. 1997), meaning an increase in the number of predators-to-prey in the edge. This is a key change in the balance of the community in the edge zone, possibly a result of the fusion of the two adjoining habitats,
with predatory species from neighbouring grass areas utilising the prey community in the forest edge.

Increased knowledge of canopy invertebrate responses to edge proximity is required beyond the 50 metre distance to elucidate how this particular component of the forest ecosystem is responding to the affects of forest fragmentation. The present research aimed to gather microclimatic data and detailed canopy invertebrate community data at set distances from sharp edges in UK conifer plantations to a depth of 100 metres. The use of relatively stable monocultures of *Picea sitchensis* and *Pinus sylvestris* plantations in the UK with sharp track edges increased the likelihood of encountering clear and definable responses to edge in the abiotic and biotic aspects. The monoculture nature of the habitat also reduced other environmental variables (e.g. understory, canopy gaps) thereby emphasising the effects of edge proximity. Collection of the whole invertebrate community allowed detailed comparison between the edge and core habitat at the order, species, density, richness, diversity and guild levels and the exploration of all aspects (individual, communal and functional) of invertebrate responses to edge proximity. The data allowed the definition of edge-effect depths, and were further used to test core-area models, calculating core area quantities in plantation patches (Chapter 4).
3.2 Methods.

Various forms of data were collected from plantations of two tree species, for the analysis of edge-effects in abiotic and invertebrate data. As discussed earlier (Chapter 2) transects were used perpendicular to plantation edge, providing the clearest form of data to show edge-effects. Additional data were also collected from the edge (0-10m) and core (80-120m) areas of *Picea sitchensis*, termed block data (Chapter 2).

Samples were collected in mid August 1995 from *P. sylvestris* and *P. sitchensis* and early September 1996 from *P. sitchensis* (Table 2.1), timed to synchronise conditions suitable for spraying with relatively high invertebrate abundances found in late summer (Speight and Wainhouse 1989). For *P. sylvestris* three replicate transects each 100 metres long were extended from edges of three different plantation patches in 1995. In the same year two transects were extended into two separate *P. sitchensis* plantation patches in Kielder Forest Northumberland (Table 2.1). Additional replicate transects were collected from *P. sitchensis* in 1996, with two further transects sampled from a single large forest patch. The three transects in *P. sylvestris* and four in *P. sitchensis* were randomly placed in different forest patches ensuring the data were not pseudo-replicated (Hurlbert 1984). True replication was also ensured by the multiple independent samples taken at the same distances from the edge but in different patches allowing the use of means. In the analysis, transects were either analysed individually or were combined, all transects from one tree species being analysed together providing mean data.
Following the first field season the need for more replicate edge and core data was highlighted and a sampling regime was initiated in 1996 to collect extra edge/core samples. Five sample trays, set out in 10 x 10 metre squares, with a tray centrally positioned and at each corner, were placed in edge (0-10m from edge) and core (80-120m from edge) habitats. Four of these blocks of five samples were taken in each habitat zone resulting in 20 additional m² ground area samples in each habitat. This increased the replication of gross edge and core data allowing improved statistical analysis of the differences between the two habitats in *P. sitchensis*. 

Three main analysis methods were used to define edge-effect patterns in both abiotic and invertebrate data. These were direct graphing methods, t-test analysis and squared and relative euclidean distance analysis. The abiotic and biotic data were analysed by all three methods to explore both gross and fine scale edge-effects. For the invertebrate data, density per m², species richness for total invertebrate diversity and for four key orders (Acarina, Araneae, Coleoptera and Collembola) and species diversity (Simpson’s index) were analysed, the selection of these orders and the use of the diversity index were discussed in Chapter 2. This elucidated the response of individual orders and species as well as the richness and diversity of the invertebrate community to edge proximity.

Direct graphing methods were inappropriate on the raw invertebrate data, as inter-sample variation was high overwhelming any responses due to edge proximity. However the more even changes found in the abiotic data were suitable for graphing, means of both temperature (°C) and relative humidity (%) were plotted against distance from plantation.
edge, highlighting general trends in the abiotic conditions with distance from plantation edge.

Because the invertebrate data were unsuitable for direct graphing, use of another technique was necessary to highlight trends in invertebrate data along the transect length and squared euclidean distances (SED) were used to show trends in the data with distance from edge. Squared (SED) and relative (RED) euclidean distances were calculated from invertebrate density per m² ground area (at order and species level) and for temperature and humidity, species richness and pre-calculated species diversity scores (Simpson's index). SED is a calculation of the square of the difference between the means of a given variable in adjacent windows (groups of samples), summed across all variables measured (Johnston et al. 1992). Window width can vary, from comparing adjacent samples a few metres apart, looking for fine scale variations along transects, to grouping many samples along transects kilometres long, to look at regional scale edge position. SEDs are then plotted against distance along transect, with high narrow peaks defining sharp edges and low wide peaks defining gradual ecotones (Johnston et al. 1992). SED however does not place an upper bound on the value of the metric (Turner et al. 1991), as it is sensitive to large aberrant values (Digby and Kempton 1987). Also samples with no species in common can exhibit smaller SED distances than samples with identical species but varying species abundances (Brunt and Conley 1990). These problems can be overcome by log transforming the data before calculation or using relative euclidean distances (Ludwig and Reynolds 1988). REDs standardise the final distance measure relative to differences in total abundance in the sampling unit. REDs were used in all calculations.
except for species diversity scores and abiotic data readings, for which SEDs were calculated. Diversity scores and abiotic readings provided a single value per sample point preventing calculation of total variation across the sample needed to standardise RED. A window width of 2 was used on the data as fine scale edge-effects were of interest on these relatively short transect lengths, this meant the square of the mean of adjacent samples was compared.

Gross variations between edge and core habitats were analysed with independent sample t-tests, comparing the means of both abiotic and biotic data between edge (0-10m) and core (80-120m) habitats. This allowed overall differences in temperature and humidity and the invertebrate communities between the edge and core habitats to be elucidated. Definition of edge and core for this analysis had to be clear. At least three samples were required to provide a mean for the analysis, so the first three samples collected from the transect (0-10m) were defined as edge for the analysis. These samples occurred in the zone (50m) considered most likely to be affected by edge proximity from previous research (Williams-Linera 1990, Young and Mitchell 1994). To compare against this the three samples at the most extreme distance from the edge samples were selected, ranging between 80 and 120 metres depending on the transect. These were beyond the often quoted edge-effect distance of 50 metres, and were considered the most likely samples to show significant differences from those at the edge.

Further resource-based analysis was performed on the invertebrate data by categorising the invertebrates into guilds (Chapter 2). The invertebrate community of each tree species
was grouped by 6 guilds (Detritivores/Fungivores, Herbivores, Parasitoids, Predators, Scavengers and Tourists) the density \( \text{m}^2 \) of each being calculated for each sample. General trends in guild densities along the length of the transects were explored by plotting graphs of guild density against distance from plantation edge, with the percentage contribution of guilds to the whole community being assessed in edge, core and the whole data set using pie charts.

Analysis (independent t-tests) was performed comparing the edge and core samples of each tree species and the difference in guild densities between the two tree species as for the original invertebrate data. More detailed guild analysis was performed on the Acarina and Coleoptera, for which more detailed identification allowed intra-order guild structure to be compiled. The Acarina species present were either predators or detritivores/fungivores, the *Pinus sylvestris* Coleoptera either detritivores/fungivores, herbivores, predators, scavengers or tourists, with just coleopteran herbivores, predators and scavengers represented in *Picea sitchensis*. Differences in intra-order guild patterns were similarly assessed between edge and core samples, species richness of the guilds within the Acarina and Coleoptera were also calculated and compared between edge and core sites. The effect of edge proximity on mean predator/prey ratios was explored by calculating a ratio of the combined predator and parasitoid guilds (predators) against all other guilds (prey). This elucidated the effects of edge proximity on the balance of predatory systems within the forest canopy.
3.3 Results.

3.3.1 Humidity edge-effects.

All plots of mean relative humidity data, the mean of three readings taken at each sample point, in *Picea sitchensis* show an increase in humidity with distance from plantation edge (Figures 3.1a-3.5a). Figure 3.1a, gives the plot of combined relative humidity (%) data for all four *P. sitchensis* transects, and shows a smooth increase to 30 metres from plantation edge, after which readings stabilise, suggesting an edge-effect depth of some 30 metres. There is a significant (P=0.014) difference in mean relative humidity between the edge and core samples for this transect (Table 3.1), relative humidity being 3% higher in the core compared to the edge. These data support the idea that relative humidity increases with depth from edge in *P. sitchensis*. Individual transects show slight variation in the pattern of humidity levels from plantation edge, but most follow the general pattern of an increased tendency towards higher humidity levels in the core. For transects 1, 3 and 4 (Figures 3.2a, 3.4a and 3.5a) in *P. sitchensis* a steady increase in humidity occurs for the complete length of the transects. However transect 2 shows a reduction in humidity from 60 to 120 metres from plantation edge (Figure 3.3a), a response to an internal gap (edge) encountered within the forest patch.

Two of the *P. sitchensis* transects, 1 and 4, show significant differences in relative humidity (Table 3.1). Transect 1 shows increased humidity in the core, with an increase of over 5% relative humidity over 120 metres. In contrast transect 4 shows an increase of
just 3% relative humidity over 100 metres. Independent sample t-tests comparing edge and core samples for these transects support the conclusion that humidity increases with distance from plantation edge.

Analysis of edge and core samples for transect 3 (Table 3.1) shows no significant difference between areas, even though superficially humidity appears to increase with distance from edge (Figure 3.4a). In this transect the most extreme change in humidity occurs over the first 5 metres, therefore the inclusion of samples at 5 and 10 metres in the analysis, which have similar figures to those of the core samples, prevent significance. The data do however suggest a sharp edge-effect of just 5 metres (Figure 3.4a). No significant differences were seen in the humidity levels of the block data collected in *P. sitchensis* between the edge (0-15m) and core (80-90m) samples (Table 3.1).

Plots of relative humidity (%) for *P. sylvestris* plantations appear more variable than those of *P. sitchensis* with humidity following the expected pattern in just one transect, 2 (Figure 3.8a), here humidity is 11% higher in the core area (Table 3.1). *Pinus sylvestris* transect 1 shows the opposite to expected response in relative humidity readings (Figure 3.7a), with nearly 10% greater humidity at the edge (Table 3.1), no internal edge was recorded for this transect so it is unclear as to why humidity is reduced in the core area. The third *P. sylvestris* transect follows a bell shape pattern in its humidity readings (Figure 3.9a), with higher ones in the mid-section of the transect, 30 to 50 metres from the edge. However humidity levels are not significantly different between the edge and core areas (Table 3.1).
Mean temperature (°C) vs. Mean relative humidity (%)

Distance (m)

A)

B)

Distance (m)
Mean temperature (°C) Mean relative humidity (%)

Distance (m)

Distance (m)

Mean temperature (°C)

Mean relative humidity (%)
Mean temperature (°C) vs. Mean relative humidity (%)

- **Graph A**: Shows a relationship between mean temperature and distance from plantation edge, with points indicating a pattern that may suggest temperature changes with distance.
- **Graph B**: Displays a similar relationship for mean relative humidity, showing variations that could reflect environmental changes.

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Distance (m) from plantation edge for *Frea stenensis* transect 3.
Mean temperature (°C) Mean relative humidity (%)

A

Mean relative humidity (%)

Distance (m)

B

Mean temperature (°C)

Distance (m)

distance (m) from plantation edge for *P. leed* sternensis transect 4.
Table 3.1. Results of independent sample t-tests comparing mean edge (0-10m) and core (80-120m) relative humidity data (%) for combined and individual transects and block data, in *Picea sitchensis* and *Pinus sylvestris* plantations.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Transect</th>
<th>Edge (0-10m)</th>
<th>Core (80-120m)</th>
<th>P. Value</th>
<th>Significance</th>
</tr>
</thead>
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<tr>
<td><em>Picea sitchensis</em></td>
<td>Combined</td>
<td>83.42 (+ SE 0.69)</td>
<td>86.67 (+ SE 0.98)</td>
<td>0.014</td>
<td>*</td>
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<tr>
<td></td>
<td>1</td>
<td>85.02 (+ SE 0.78)</td>
<td>90.75 (+ SE 0.05)</td>
<td>0.018</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>82.7 (+ SE 0.38)</td>
<td>83.12 (+ SE 0.9)</td>
<td>0.691</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>80.48 (+ SE 1.27)</td>
<td>84.04 (+ SE 0.19)</td>
<td>0.104</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>85.48 (+ SE 0.23)</td>
<td>88.79 (+ SE 0.32)</td>
<td>0.001</td>
<td>***</td>
</tr>
<tr>
<td>Block</td>
<td>Combined</td>
<td>81.27 (+ SE 1.68)</td>
<td>79.59 (+ SE 2.36)</td>
<td>0.569</td>
<td>NS</td>
</tr>
<tr>
<td><em>Pinus sylvestris</em></td>
<td>Combined</td>
<td>64.76 (+ SE 5.13)</td>
<td>66.57 (+ SE 4.43)</td>
<td>0.792</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>1#</td>
<td>64.7 (+ SE 0.51)</td>
<td>55.91 (+ SE 0.29)</td>
<td>0.000</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>47.14 (+ SE 1.59)</td>
<td>59.7 (+ SE 0.24)</td>
<td>0.001</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>82.43 (+ SE 1.12)</td>
<td>84.11 (+ SE 1.02)</td>
<td>0.329</td>
<td>NS</td>
</tr>
</tbody>
</table>

SE = Standard error of the mean, NS = non significance, * = P< 0.05, ** = P< 0.01 and *** = P< 0.001.

# Transect showing opposite trend, lower relative humidity (%) in core.
Combined data for the three *Pinus sylvestris* transects show no significant variation in relative humidity between edge and core samples (Table 3.1), this lack of significance in the combined data is a result of two of the transects having completely opposing trends. Transect 1 with higher humidity levels at plantation edge, and transect 3 with higher humidity in the middle section of the transect than at either of the two ends. The combined plot of relative humidity data shows a slight bell shaped curve, with a higher and more stable area of humidity in the mid-samples (Figure 3.6a).

These relative humidity results in general follow a trend of increased humidity in plantation core for both tree species but particularly in *P. sitchensis*. The more stable plantation structure of *P. sitchensis*, with even dense stands may increase the likelihood of finding smooth edge-effects particularly in relative humidity, whereas the low number of significant results in *P. sylvestris* and variability of graph profiles could be an indication of the high variation found in relative humidity due to the more open and variable canopy structure of the latter genus.

It appears that the most extreme changes in relative humidity in the two tree species occur over the first few metres of the transect but actual position of edge-effect depth, i.e. the point of maximum contrast, is hard to define from this analysis. Squared euclidean distances will be used to elucidate these (see below).

3.3.2 Temperature edge-effects.
No significant difference was reported in temperature (°C) between the edge and core data of the combined *P. sitchensis* transects (Table 3.2), although the plot of the data (Figure 3.1b) shows a tendency towards a positive edge-effect in temperature, with increased values at the edge. Lack of significance is due to the high variation between individual transects. When analysed independently transects 1 and 4 show significant variation in temperature readings (Table 3.2), showing a clear reduction of *circa* 1°C in temperature away from plantation edge (Figures 3.2b and 3.5b). Transect 2 shows a slight bell shaped curve (Figure 3.3b) which is similar, but in reverse, to that seen in the humidity readings of the same transect (Figure 3.3a). This increase in temperature in the core area is a response to the internal edge reported for this transect.

Although transect 3 does not show a significant result in its temperature readings (Table 3.2), a clear edge-effect is discernible from the plot (Figure 3.4b). The lack of significance is due to a slight increase in temperature readings in the core samples, and the rapid decline in temperature at the edge, with the zero metre sample appearing to be the only significantly higher temperature reading to all the others (Figure 3.4b). No significant analysis of the edge and core block data collected in *P. sitchensis* occurred (Table 3.2), if anything, the trend is reversed with slightly higher temperature readings in the core area.

Due to high variation between *P. sylvestris* transects the combined transect data show no significant variation in mean temperature between edge and core sites (Table 3.2), although the graph of the combined data would suggest otherwise (Figure 3.6b), showing
A graph shows the mean relative humidity (%) as a function of distance (m) from the plantation edge for *F. thas sylvestris* is transect 2.

B graph shows the mean temperature (°C) as a function of distance (m) from the plantation edge for *F. thas sylvestris* is transect 2.
distance (m) from plantation edge for Pinus sylvestris transect 5.
Table 3.2: Results of independent sample t-tests comparing mean edge (0-10m) and core (80-120m) temperature (°C) data, for combined and individual transects and block data, in *Picea sitchensis* and *Pinus sylvestris* plantations.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Transect</th>
<th>Edge (0-10m)</th>
<th>Core (80-120m)</th>
<th>P. Value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea sitchensis</em></td>
<td>Combined</td>
<td>14.94 (±SE 0.54)</td>
<td>14.51 (±SE 0.63)</td>
<td>0.611</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>14.38 (±SE 0.16)</td>
<td>13.5 (±SE 0.02)</td>
<td>0.006</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>17.29 (±SE 0.08)</td>
<td>17.49 (±SE 0.12)</td>
<td>0.248</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>12.44 (±SE 0.26)</td>
<td>11.86 (±SE 0.05)</td>
<td>0.092</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>15.65 (±SE 0.06)</td>
<td>15.19 (±SE 0.03)</td>
<td>0.003</td>
<td>**</td>
</tr>
<tr>
<td>Block</td>
<td>Combined</td>
<td>13.99 (±SE 0.38)</td>
<td>14.83 (±SE 0.56)</td>
<td>0.229</td>
<td>NS</td>
</tr>
<tr>
<td><em>Pinus sylvestris</em></td>
<td>Combined</td>
<td>19.82 (±SE 0.93)</td>
<td>19.14 (±SE 1.12)</td>
<td>0.647</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>1#</td>
<td>21.86 (±SE 0.11)</td>
<td>23.39 (±SE 0.05)</td>
<td>0.000</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>21.42 (±SE 0.6)</td>
<td>18.17 (±SE 0.07)</td>
<td>0.006</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>16.17 (±SE 0.1)</td>
<td>15.84 (±SE 0.3)</td>
<td>0.032</td>
<td>*</td>
</tr>
</tbody>
</table>

SE = Standard error of the mean, NS = non significance, * = P< 0.05, ** = P< 0.01 and *** = P< 0.001.

# Transect showing opposite trend, lower temperature (°C) at edge.
a drop of almost 1.5 °C over 25 metres from transect edge. Independently all three transects show significant differences between edge and core samples, with both positive and negative responses to edge proximity (Table 3.2).

Transect 1 has the reverse to expected temperature readings (Figure 3.7b), as it did with humidity, showing increased temperatures, by 1.5 °C, in the core samples (Table 3.2). These reversed results in the humidity and temperature data for the transect are unaccountable, as canopy cover was even over the length of the transect and no clear internal edge was present. The transect was west facing compared to the southerly orientation of the other two *P. sylvestris* transects, although this should not result in a complete reversal of the expected pattern in the abiotic data, a more westerly orientation would simply reduce the expected depth of the edge-effect (Matlack 1993).

A drop of circa 3 °C from the edge to the core habitat is seen for transect 2 in *P. sylvestris* (Table 3.2, Figure 3.8b), this follows the expected pattern of increased temperature at the exposed plantation edge. A much smaller but equally significant result is seen between the edge and core samples for transect 3 (Table 3.2). However the plot of the transect shows an interesting pattern (Figure 3.9b) with an extreme drop in temperature to 40 metres from plantation edge, followed by an apparent recovery in temperature levels over the last 50 metres of the transect. Again this is a similar but reversed pattern to that seen in the humidity data and could suggest the presence of an internal edge in the plantation.
A number of the transects show significant variation in temperature with distance from edge, two in \textit{P. sitchensis} (transects 1 and 4) and two in \textit{P. sylvestris} (transects 2 and 3). In general overall decline in temperature readings with distance from edge are small, in the region of 1°C. Only one transect shows a significant opposite trend, \textit{Pinus sylvestris} (1), as it did in the humidity, this highly significant but completely opposing trend in the abiotic data is unaccountable.

3.3.3 Invertebrate edge-effects.

3.3.3.1 Positive mean density responses to edge.

Seven taxa respond positively to edge proximity in \textit{Picea sitchensis} plantations, showing higher densities in edge samples, no taxon shows any significant variation in density between edge and core for \textit{Pinus sylvestris} plantations. Coleoptera shows the most consistent response to edge proximity in \textit{P. sitchensis}, with significant results for the combined transects, transect 1 and block data (Figure 3.10 and Table 3.3). Mean density of Coleoptera is almost 3 times higher in the edge, for the combined data, and 6 ½ times higher for transect one with densities of up to 40 per m², a result of high numbers of Coccinellidae and Staphylinidae. The block data shows a lower difference in density levels between the edge and core areas (Table 3.3), most of which is accounted for by one species, \textit{Aphidecta obliterata} (Coccinellidae), which also shows significantly higher densities in the edge samples (Figure 3.11). Increased mean density for the Coleoptera in the block data is also associated with an increase in species richness at the edge (Figure
mean richness being 1.3 times higher. *P. sitchensis* edge samples are showing increased coleopteran densities and richness which are not found in *P. sylvestris* samples, accounted for by large numbers of Coccinellidae.

Dipteran density also responds positively to edge proximity, with 1.9 and 1.4 times higher densities in the edge for transect 3 and the block data respectively (Figures 3.13-3.14). Hemipteran density is over five times higher in the edge samples compared to the core samples of transect 4 in *P. sitchensis* (Figure 3.15), this increased density at the edge could be a response to the greening of the vegetation at plantation edge providing increased food sources (Williams-Linera 1990, Chen et al. 1992). One family of spiders, the Linyphiidae (Araneae), responds positively to edge proximity (Figure 3.16) in the block data of *P. sitchensis*, with 1.7 times the densities in edge samples.

Interestingly even though mean densities of Collembola are significantly higher in the core area for both tree species (Figures 3.17 and 3.18), one species *Sminthurus fuscus* shows higher density in the edge samples of the *P. sitchensis* block data (Figure 3.19). This highlights ordinal level responses to edges may be very different for individual species within the order.

### 3.3.3.2 Positive species richness and diversity responses to edge

As mentioned, species richness of Coleoptera is higher in the edge samples of the block *P. sitchensis* data (Figure 3.12) and three other significant results are also reported for
Table 3.3. Results of independent sample t-tests comparing mean invertebrate density (m$^2$) between edge (0-10m) and core (80-120m) samples, for combined and individual transects in *Picea sitchensis* and *Pinus sylvestris* plantations.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Transect</th>
<th>Taxon</th>
<th>Edge (0-10m)</th>
<th>Core (80-120m)</th>
<th>P. Value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea sitchensis</em></td>
<td>1</td>
<td>Coleoptera</td>
<td>36.67</td>
<td>5.67</td>
<td>0.027</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Block</td>
<td>Coleoptera</td>
<td>10.32</td>
<td>7.64</td>
<td>0.026</td>
<td>*</td>
</tr>
<tr>
<td><em>Pinus sylvestris</em></td>
<td>Combined</td>
<td>Chamobates sp.</td>
<td>0.33 (±SE 0.33)</td>
<td>16.89 (±SE 7.13)</td>
<td>0.049</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Anystis sp.</td>
<td>0 (±SE 0)</td>
<td>2.33 (±SE 0.33)</td>
<td>0.02</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Drapetisca socialis</td>
<td>0 (±SE 0)</td>
<td>4.33 (±SE 1.45)</td>
<td>0.041</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Chamobates sp.</td>
<td>0 (±SE 0)</td>
<td>3.33 (±SE 0.33)</td>
<td>0.01</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Cymbaaermaeus sp.</td>
<td>4.33 (±SE 1.45)</td>
<td>36 (±SE 10.44)</td>
<td>0.04</td>
<td>*</td>
</tr>
</tbody>
</table>

SE = Standard error of the mean, * = P < 0.05, ** = P < 0.01.
Figure 3.11. Mean *Aphidecta obliterata* (Coleoptera) density (m²) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples (P=0.003 indep. t-test).
Mean species richness (m²)

edge (+1 SE mean) and core (50-90m) samples (t = 0.054 indep. t-test).
Figure 3.14. Mean dipteran density (m²) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples (P=0.027 indep. t-test).
Figure 3.16. Mean Linyphiidae (Araneae) density ($m^2$) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples ($P=0.04$ indep. t-test).
Figure 3.18. Mean collembolan density (m²) in combined *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.031 indep. t-test).
this tree species. Total species richness, across all invertebrates increased by 1.2 times in the edge samples of the block data of *P. sitchensis* (Figure 3.20). Total species richness is also supported by the result of the analysis of species diversity scores (Simpson’s index), total species diversity is 1.5 times higher in the edge samples compared to the core samples in transect 2, *P. sitchensis* (Table 3.4). Acarina species richness also shows a slight but significant increase in the edge samples for both the combined and block data, being 1.3 and 1.6 times higher respectively (Figures 3.21 and 3.22). No significant differences are seen in the species diversity between edge and core samples in any *P. sylvestris* transects.

Positive responses to edge proximity including higher densities, species richness and diversity in edge samples, are only significant in the *P. sitchensis* plantations, no taxa respond in a significantly positive way to the edge area of *P. sylvestris* plantations (Table 3.5). The Coleoptera appear to be exceptionally responsive to edge proximity in *P. sitchensis*, with higher densities and species richness in the edge samples. Potential prey sources of the predatory Coleoptera, such as the Coccinellidae which are common in the edge samples, also have increased densities in edge samples (Hemiptera). Diptera and Araneae are two important groups also responding to the edge and one species of Collembola have higher densities in the edge. As well as increased Coleopteran and Acarina species richness in the edge samples total invertebrate species richness and diversity are increased in the edge compared with the core area.
3.3.3.3 Positive guild responses to edge.

Two guilds respond to edge proximity in *P. sitchensis* (Table 3.6), the scavengers showing consistently higher densities, at most twice as dense, in the edge samples of the combined, block and transect 3 data sets. Herbivores also show considerably higher densities in the edge samples of *P. sitchensis* (Table 3.6), a reflection of the high densities of Hemiptera in the area, responding to the greening of the edge vegetation. As in the case of invertebrate densities the guild densities show no positive responses to edge habitat in *P. sylvestris*, with guild densities being similar between edge and core samples.

Plots of mean guild densities against distance from plantation edge show little pattern in either tree species, inter sample variation being high. Although the tourist guild in *P. sitchensis* does appear to show higher densities in the very edge samples (0m) of the transect (Figure 3.23), the result is not significant due to the rapid decline in densities after 0 metres. The pattern is not repeated in the *P. sylvestris* transect (Figure 3.24) which shows high densities throughout the length of the transect.

Predator/prey ratios show no significant differences between edge and core samples in either tree species with similar values in the two habitat types. Mean predator/prey ratios of 0.31 and 0.27 for edge and core samples respectively were calculated in *P. sitchensis*, with values of 0.14 and 0.21 for *P. sylvestris*. Plots of mean predator/prey ratio against distance from edge show no pattern within either tree species, ratios being similar throughout the lengths of the transects.
Detailed analysis of the Acarina guilds between edge and core samples shows no positive responses to edge proximity between the two habitats in *P. sitchensis*, densities of detritivores/fungivores and predators being similar in the two habitats, detritivores being more abundant than predators in both areas. Similarly no significant positive effects to edge proximity are seen for Acarina guild densities in *P. sylvestris*. Acarina guild species richness similarly shows no positive responses to edge proximity in *P. sylvestris* but does in *P. sitchensis* with both the detritivores/fungivores and predators showing higher richness in the edge samples (Figures 3.25-3.26).

The Coleoptera has representatives of many more guilds than the Acarina with coleopteran herbivores, predators and scavengers in *P. sitchensis*, with the addition of detritivores/fungivores and tourists in *P. sylvestris*. Significant responses to edge proximity are only seen in the *P. sitchensis* samples, with the herbivorous and predatory coleopteran guilds showing higher densities in the edge samples (Table 3.7), some core samples showing no coleopteran herbivores at all. Along with the increased densities of herbivorous coleoptera in the edge samples the same area shows increased species richness for this guild (Figure 3.27), a result of the lack of herbivorous Coleoptera in the core samples.

Comparison of the percentage contribution to the population various guilds made in the edge and core habitats by pie charts shows very little variation, either for total invertebrate guilds or those of the Acarina and Coleoptera. Detritivore and predatory guilds in the Coleoptera contribute more to the community in the edge samples than the core (Figure
Mean species richness ($m^2$) for edge (0-10m) and core (80-90m) samples ($P<0.000$ indep. t-test).
Table 3. 4. Results of independent sample t-tests comparing mean species diversity scores (Simpson's index) for total invertebrate capture and order level diversity in edge (0-10m) and core (80-120m) samples, for combined and individual transects, in *Picea sitchensis* and *Pinus sylvestris* plantations.

<table>
<thead>
<tr>
<th>Position</th>
<th>Tree Species</th>
<th>Transect</th>
<th>Taxa</th>
<th>Edge (0-10m)</th>
<th>Core (80-120m)</th>
<th>P. Value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Edge</td>
<td><em>Picea sitchensis</em></td>
<td>2</td>
<td>Total</td>
<td>5.32 (±SE 0.27)</td>
<td>2.72 (±SE 0.2)</td>
<td>0.001</td>
<td>***</td>
</tr>
<tr>
<td>Core</td>
<td><em>Picea sitchensis</em></td>
<td>3</td>
<td>Coleoptera</td>
<td>0.04 (±SE 0.02)</td>
<td>0.14 (±SE 0.02)</td>
<td>0.033</td>
<td>*</td>
</tr>
<tr>
<td>Core</td>
<td><em>Pinus sylvestris</em></td>
<td>Combined</td>
<td>Total</td>
<td>3.88 (±SE 0.64)</td>
<td>6.07 (±SE 0.73)</td>
<td>0.038</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>Acarina</td>
<td>1.02 (±SE 0.20)</td>
<td>2.5 (±SE 0.25)</td>
<td>0.000</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Acarina</td>
<td>0.33 (±SE 0.33)</td>
<td>3.09 (±SE 0.52)</td>
<td>0.011</td>
<td>*</td>
<td></td>
</tr>
</tbody>
</table>

SE = Standard error of the mean, * = P< 0.05, ** = P< 0.01 and *** = P< 0.001.
Mean Acarina species richness (m²) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples (P=0.022 indep. t-test).

**Figure 3.22.** Mean Acarina species richness (m²) in block *Picea sitchensis* edge (0-10m) and core (80-90m) samples (P=0.000 indep. t-test).
Table 3.5. Review of positive and negative invertebrate responses to edge proximity in *Picea sitchensis* and *Pinus sylvestris* plantations.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>+ Edge Response</th>
<th>- Edge Response</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea sitchensis</em></td>
<td>Acarina</td>
<td>Collembola</td>
</tr>
<tr>
<td></td>
<td>Linyphiidae (Araneae)</td>
<td><em>Entomobrya nivalis</em> (Collembola)</td>
</tr>
<tr>
<td></td>
<td>Coleoptera</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Aphidecta obliterata</em> (Coleoptera)</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Sminthurus fuscus</em> (Collembola)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Diptera</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hemiptera</td>
<td></td>
</tr>
<tr>
<td><em>Pinus sylvestris</em></td>
<td>Acarina</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Drapetisca socialis</em> (Araneae)</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Leptophantes expunctus</em> (Araneae)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Collembola</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Entomobrya nivalis</em> (Collembola)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Neuroptera</td>
<td></td>
</tr>
</tbody>
</table>
Table 3.6. Results of independent sample t-tests comparing mean guild density (m$^2$) of all arthropods between edge (0-10m) and core (80-120m) samples, for combined, individual transects and block data, in *Picea sitchensis*. No significant differences were seen in guild densities (m$^2$) between edge and core samples for *Pinus sylvestris* transects.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Transect</th>
<th>Guild</th>
<th>Edge (0-10m)</th>
<th>Core (80-120m)</th>
<th>P. Value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea sitchensis</em></td>
<td>Combined</td>
<td>Scavengers</td>
<td>38.97 (±SE 3.93)</td>
<td>26.81 (±SE 3.46)</td>
<td>0.024</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Scavengers</td>
<td>39.00 (±SE 2.00)</td>
<td>20.33 (±SE 3.84)</td>
<td>0.013</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Block</td>
<td>Scavengers</td>
<td>34.85 (±SE 3.31)</td>
<td>21.45 (±SE 2.55)</td>
<td>0.003</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Herbivores</td>
<td>35.67 (±SE 3.38)</td>
<td>6.00 (±SE 1.73)</td>
<td>0.001</td>
<td>***</td>
</tr>
</tbody>
</table>

SE = Standard error of the mean, * = P<0.05, ** = P<0.01 and *** = P<0.001.
Figure 3.24. Mean tourist guild densities (m²) with distance from plantation edge (m) for *Pinus sylvestris* transects.
3.28), with the tourist guild being completely absent from the edge samples. These differences are not highlighted by the t-test analysis but reflect some differences in the patterns of the coleopteran guilds between edge and core habitat in *P. sylvestris*.

### 3.3.3.4 Negative mean density responses to edge.

The Collembola are the only taxon to show significant response in mean density to the core area of *Picea sitchensis* (Transect 2). Total collemboalan density is 3 times higher in the core area compared to the edge (Figure 3.17); a response almost completely accounted for by the species *Entomobrya nivalis* (Figure 3.28), a widespread but environmentally sensitive species (Andre 1985, Hopkin 1997). All other taxa either show no response to core area or have higher mean densities in the edge samples (Table 3.5).

A number of taxa however show a positive response to core conditions in *P. sylvestris* plantations. Acarina seem to respond greatly to core conditions both at the order and species level. Mean Acarina density is 16 times higher in the core area of transect 1 (Figure 3.29), reaching levels of 30 plus individuals per m². Throughout all the Acarina results densities are exceptionally low in the edge samples. *Chamobates sp.* (Acarina: Oribatida) seems to show a considerable preference for core areas being 51 times denser in the core of the combined transect data, and only occurring in the core samples of transect 3 (Table 3.3). Another species of Acarina, *Anystis sp.* (Prostigmata) shows an extreme preference for core samples in transect 1, being found in no edge samples (Table 3.3). This species is however found in the edge samples of the other transects, so it does
not have a total preference for core habitat. The final mite species to show a core preference in the *P. sylvestris* data is *Cymbaeremaeus sp.* (Oribatida) which has a density in the core area of transect 3, 8 times that of the edge (Table 3.3). So total Acarina and various species of Acarina show increased preference for core conditions.

The Collembola as in the *P. sitchensis* transects show a clear response to the core areas of *P. sylvestris*. For the combined transect data total collembolan density is 7 times higher in the core (Figure 3.18), whilst in transect 3 it is 9 ½ times higher (Figure 3.30), with densities in the region of 50 to 100 per m² ground area (core). This increased density in the core area of *P. sylvestris* for collembola is accounted for, almost completely, by one species *Entomobrya nivalis* (Figure 3.31) as it was for *P. sitchensis*, *E. nivalis* returning a density of 100 individuals per m² ground area.

Two species of spider show significantly higher densities in the core areas of *P. sylvestris*, these are *Drapetisca socialis* (Linyphiidae) and *Lepthyphantes expunctus* (Linyphiidae) (Figures 3.32 and 3.33), both of which are woodland species (Roberts 1987). *Drapetisca socialis* shows responses in both the combined transect data where its density is 19 times higher in the core (Figure 3.32) and transect 1 data where it only occurs in the core samples (Table 3.3). Mean density of *L. expunctus* is 7 times higher in the core area of transect 2 (Figure 3.33). The only other taxon to show a response to core conditions in *P. sylvestris* is the Neuroptera whose density is 3 times higher in the core area of the combined transect data (Figure 3.34).
3.3.3.5 Negative species richness and diversity responses to edge.

Along with the considerable response in mean density to core conditions, the Acarina also show increased levels of species richness in the core areas of *Pinus sylvestris* plantations. Acarina species richness levels are 1.6 times higher in the core area of the combined transect data and 5 ½ times higher in the core of transect one (Figure 3.35 and 3.36). Acarina species diversity levels (Simpson’s index) also show significantly higher rates in the core areas of *P. sylvestris*. For the combined *P. sylvestris* data diversity levels are over twice as high in the core area as the edge (Table 3.4), and nine times greater in the transect 1 data (Table 3.4). Total invertebrate species diversity also shows increased levels in the core area for the combined *P. sylvestris* data, being 1.5 times higher in the core (Table 3.4). Only one species’ diversity analysis is significant for *Picea sitchensis* data, the Coleoptera from transect 3 showing increased diversity by 3 times in the core area (Table 3.4).

3.3.3.6 Negative guild responses to edge.

Few positive responses to core habitat are seen in the guilds compared to the edge habitat, with no guild densities being higher in the core habitat. However in *P. sylvestris* the Acarina predatory guild shows higher densities in the core area of transect 1 (Figure 3.37), no predatory Acarina being found in the edge samples. This trend is followed throughout the data set with predatory and detritivore/fungivore Acarina showing higher but not significantly higher densities in core areas, a result of the higher densities of
Table 3.7. Results of independent sample t-tests comparing mean coleopteran guild density (m²) between edge (0-10m) and core (80-120m) samples, for combined, individual transect and block data, in *Picea sitchensis*. No significant differences were seen in coleopteran guild density (m²) between edge and core samples for *Pinus sylvestris* transects.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Transect</th>
<th>Coleopteran Guild</th>
<th>Edge (0-10m)</th>
<th>Core (80-120m)</th>
<th>P. Value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea sitchensis</em></td>
<td>Combined</td>
<td>Herbivores</td>
<td>0.41 (± SE 0.13)</td>
<td>0.00 (± SE 0.00)</td>
<td>0.003 **</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>Predators</td>
<td>6.91 (± SE 1.62)</td>
<td>2.81 (± SE 0.46)</td>
<td>0.020 *</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Predators</td>
<td>30.33 (± SE 6.17)</td>
<td>3.33 (± SE 0.88)</td>
<td>0.046 *</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Block</td>
<td>Herbivores</td>
<td>0.35 (± SE 0.13)</td>
<td>0.00 (± SE 0.00)</td>
<td>0.015 *</td>
<td>*</td>
</tr>
</tbody>
</table>

SE = Standard error of the mean, * = P < 0.05, ** = P < 0.01.
Figure 3.26. Mean species richness (m²) of Acarina predators between edge and core samples in *Picea sitchensis* plantations.
Mean species richness (± 2 SE)

edge

core
(A) and (B) core (60-120m) communities of combined Pinius sylvestris samples.
Figure 3.30. Mean Acarina density ($m^2$) in transect 1 *Pinus sylvestris* edge (0-10m) and core (80-120m) samples ($P=0.041$ indep. t-test).
Figure 3.32. Mean *Entomobrya nivalis* (Collembola) density (m²) in transect 3 *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.001 indep. t-test).
Figure 3.34. Mean Leptophantes expunctus (Aranae) density (m$^2$) in transect 2 Pinus sylvestris edge (0-10m) and core (80-120m) samples ($P=0.013$ indep. t-test).
Mean density 

![Diagram showing mean density comparison between edge and core samples with error bars indicating +/- 1 SE mean.](image)

(0-10 m) and core (60-120 m) samples (t = 0.041 indep. t-test).
Figure 3.37. Mean Acarina species richness (m$^2$) in transect 1 *Pinus sylvestris* edge (0-10m) and core (80-120m) samples (P=0.003 indep. t-test).
Acarina in core areas of *P. sylvestris*. The only other response to plantation core is by the detritivore Acarina which show higher species richness in the core area of *P. sylvestris*. So *P. sylvestris* core areas show particularly high densities of a few species of predatory Acarina and a greater species richness of detritivore species compared to the edge samples although they share overall similar densities of Acarina.

3.3.4 Squared and relative euclidean distance edge-effects.

3.3.4.1 Abiotic data.

Squared euclidean distance (SED) plots clearly define an edge-effect in three of the *Picea sitchensis* transects and two of the *Pinus sylvestris* transects (Figures 3.39-3.43). These plots show sharp contrast (peaks) between samples in the edge region. A number of these plots highlighting edge-effects, are those transects that show significant results in the t-tests between their edge and core data (see above).

The combined SED plot in *P. sitchensis*, which includes both relative humidity (%) and temperature (°C) shows the highest point of contrast at 2.5 metres, suggesting the greatest difference between abiotic conditions is between the 0 and 5 metre samples (Figure 3.38). After this point squared euclidean distance values are at a constant low level, suggesting low inter sample contrast. The combined *P. sitchensis* abiotic SED data therefore reflect a strong edge-effect over the first 5 metres of the forest habitat, with the balance of temperature and relative humidity stabilising beyond this point.
Individually the *P. sitchensis* transect SED plots show more variation, transects 2 and 4 having a variable pattern in SED values with peaks and troughs throughout the length of the transect. Transects 1 and 3 show more of an edge response with increased levels of contrast in the SED values close to forest plantation edge. The point of highest contrast in Kielder transect 1 (Figure 3.39), with twice the contrast of any other point on the transect, is at 2.5 metres, again supporting a strong edge-effect in the first 5 metres of *P. sitchensis* transects. However other significant areas of contrast occur further into the Kielder 1 transect, at 12.5 and to a lesser extent at 25 metres (Figure 3.39). These areas of high contrast further into the plantation suggest that less extreme variations are occurring in abiotic data to a greater depth than the first 5 metres. Subtle contrasts in abiotic data are occurring to a depth of circa 30 metres in this *P. sitchensis* transect, so abiotic conditions are not stabilising until 30 metres. In contrast to this the third *P. sitchensis* transect shows a single clear contrast in its squared euclidean distance data, similar to that of the combined data (Figure 3.40). Again this point of high contrast is situated at the 2.5 metre mark suggesting a strong and rapid change in abiotic conditions at the very edge of *P. sitchensis* plantations, with consistent conditions beyond this point.

*Pinus sylvestris* transects in general are more variable in their abiotic factors than *P. sitchensis* (see above), due to the more open canopy, so patterns in SED values are more difficult to establish. This high variation between transects has resulted in a very variable SED plot for the combined data which shows no particular pattern. The SED plot for *P. sylvestris* transect 1 shows two main points of contrast at 2.5 and 75 metres from
plantation edge (Figure 3.41). The highest point of contrast, at the internal position (75m) could be explained by this transect showing completely reversed abiotic conditions, with higher temperature and lower humidity in the core region. This SED plot suggests, as did the other data that an internal edge is present resulting in opposed abiotic conditions and a high point of contrast in the SED values. The second highest point of contrast at 2.5 metres (Figure 3.41) shows a clear edge-effect response in the abiotic data to the original plantation edge, as expected, although of a reversed nature with high humidity and low temperature.

*Pinus sylvestris* transect 2 shows regular profiles in its temperature and humidity data (Figures 3.8a and b) and highly significant results comparing edge and core samples (Table 3.1 and Table 3.2). These results are supported by the SED plot which shows high levels of contrast over the first 30 metres of the transect (Figure 3.42). The highest point of contrast is at 7.5 metres, then 17.5 and finally 27.5 metres, after which the SED profile is practically flat suggesting little contrast in abiotic readings between adjacent samples, and that a steady state of abiotic conditions has been reached 30 metres from plantation edge.

Although previous research has found that abiotic edge-effects extend many metres into the forest habitat (Matlack 1993, Chen *et al.* 1995, Ozanne *et al.* 1997), from this data it can only be established that very clear edge-effects are present in the first 5 metres of forest habitat. Although some transects namely *P. sitchensis* transect 1 and *P. sylvestris* transect 2 may reflect an edge-effect of up to 30 metres.
3.3.4.2 Positive invertebrate responses to edge.

Few invertebrate orders and no total invertebrate density respond with clear patterns in their RED plots. The majority of the plots show peaks and troughs throughout the length of the transect. Only two invertebrate density plots show any clear pattern that highlights the presence of contrast in the data. Figure 3.43 shows the RED plot of Acarina density with distance from plantation edge in *P. sitchensis* (transect 1), the highest RED value being at 2.5 metres, although values for the rest of the transect show quite high contrast. This point of high contrast between the 0 and 5 metre samples suggests a rapid change in density of Acarina, the raw data showing an increase in density in the 5 metre sample compared to the very edge sample. Acarina density appears to be responding negatively to edge proximity, with lower densities in the very edge sample. However no significant result was seen between t-test analysis of the edge and core samples, suggesting no gross edge-effect in Acarina density, the RED plot suggests a subtler 0 to 5 metre density edge-effect.

The only other density data to show a really clear point of contrast in its length is the plot of RED Coleoptera density for *P. sitchensis* transect 2. Again the point of highest inter sample variation is at 2.5 metres (Figure 3.44) followed by a low area of RED values before peaks start to appear towards the core. This high contrast is due to a low density of beetles in the sample at 5 metres compared to those surrounding it. The more level section of the graph (10-25m) is reflected in the data by relatively high densities of beetles before the density declines towards the core. These lower values could be
resulting in the higher RED values. This general pattern of difference between edge and core samples, with increased densities of beetles at the edge is supported by the t-test results (Figure 3.10). Here the RED plot is reflecting a change in coleopteran density with distance from edge, also supported by other analysis.

All other analysis of Acarina, Araneae, Coleoptera, Collembola and total invertebrate densities shows an absence of consistent patterns of response to edge habitats. However four SED plots show considerable response to edge area for species diversity in both Acarina and total invertebrate diversity.

*Picea sitchensis* transect 1 shows two significant results in total invertebrate species diversity and that of the Acarina. The most extreme point in SED is at the 2.5 metre mark for total invertebrate diversity (Figure 3.43). The sample at 5 metres has more species (18) than the zero metre sample (14), but the zero metre sample is more equitable resulting in a higher diversity index. Contrast points continue for a distance down the transect with another point of high contrast at 35 metres, suggesting that reasonable variation in diversity is occurring up to the 30 to 40 metre mark. This transect shows an increase in species diversity at plantation edge to a distance of 30 metres. This SED result is backed up in general by the t-test results for both diversity and richness, for at least some of the *P. sitchensis* transects total diversity and richness were higher in the edge samples than the core.
Fleu sitchensis transect abiotic data, showing highest contrast between 6 and 9 metre samples.
Figure 3.41. Mean squared euclidean distance (SED) plotted against distance (m) for *Picea sitchensis* transect 3 abiotic data, showing highest contrast between 0 and 5 metre samples.
Figure 3.43. Mean squared euclidean distance (SED) plotted against distance (m) for *Pinus sylvestris* transect 2 abiotic data, showing high areas of contrast over the first 30 metres of the transect.
Total invertebrate diversity also shows an edge-effect pattern in the SED plot for *P. sylvestris* transect 2. The transect pattern is a little (Figure 3.46), but SED values are generally higher over the first 20 metres, reflecting higher contrast between samples. From 20 metres onwards contrast is lower reflecting more stable diversity levels in those samples, the core samples although showing low contrast in the SED plot, have higher diversity values. So diversity appears to be more random at the edge with extreme variation, before settling down to a more constant and higher level of diversity in the core area of *P. sylvestris*. This is reflected in both the species diversity data in various *P. sylvestris* transects which show significantly higher values in the core (Table 3.4).

Only one order shows any edge responses in its diversity data, that is the Acarina which shows SED contrasts in the edge of *P. sitchensis* transects 1 and 4. The highest point of contrast is at 2.5 metres for transect 1, with a slight increase in contrast again towards the core samples (Figure 3.47). Contrast is high at the edge of the transect due to low diversity figures in the very edge sample. This sample has low species number and relatively low equatability, so the number of individuals is unevenly distributed between species. This transect suggests an edge-effect of 2.5 metres in Acarina species diversity.

Acarina diversity in *P. sitchensis* transect 4 (Figure 3.48) shows very high contrast at the edge of the plantation then low variation for the rest of the transect. SED figures are highest at 7.5, 12.5 and 17.5 metres from transect edge, this is due to low equatability in these samples and high species number, resulting in high diversity index figures. After this area of increased diversity at the edge, the number of species in samples declines and
equatability increases reducing diversity values, and increasing similarity between samples. This transect shows a clear edge-effect with high diversity in Acarina at the edge of the transect and lower diversity in the core area from 25 metres into the transect. This result is not supported by the t-test results which show no significance in Acarina diversity in *P. sitchensis*, however species richness is significantly higher in the edges of some *P. sitchensis* transects (Figure 3.21 and 3.22) which lends some credence to this result.

3.3.4.3 Negative invertebrate responses to edge.

No SED or RED plots show a clear pattern of increased contrast at the internal area of transects for mean density data. The bulk of the graphs show no overall pattern with high contrast throughout their length. However one graph is of interest (Figure 3.50), the plot of RED values for collembolan mean density in *P. sylvestris* transect 3, shows an area of very high contrast in its mid-section, between 30 and 60 metres. This is due to a sudden increase in density of Collembola, particularly *Entomobrya nivalis*; in fact no other species of Collembola occur in the data set until the samples at 35 metres. This sudden increase leads to high contrast between these samples and those towards the end of the transect at 90 metres. These higher RED values and their underlying cause, increased density of Collembola, is clearly demonstrated by the significant results found when comparing the edge and core samples for these invertebrates (Figures 3.17 and 3.18). Here the RED plot is clearly demonstrating its function of highlighting high areas of contrast, in this case the fact that Collembola show a clear edge-effect of 30 metres in *P.*
Figure 3.45. Mean relative euclidean distance (RED) plotted against distance (m) for *Picea sitchensis* transect 2 Coleoptera density (m$^2$) data, showing high contrast between 0 and 5 metre samples.
Figure 3.47. Mean squared euclidean distance (SED) plotted against distance (m) for *Pinus sylvestris* transect 2 invertebrate diversity (Simpson's index) data (m²), showing high contrast over the first 20 metres.
Figure 3.49. Mean squared euclidean distance (SED) plotted against distance (m) for *Picea sitchensis* transect 4 Acarina species diversity (Simpson's index) data (m²), showing high contrast between 0 and 5 metre samples.
transsect 5 cormobolan density data (m$^{-3}$), showing high contrast in the mid-section of the transect.
Figure 3.52. Mean squared euclidean distance (SED) plotted against distance (m) for *Pinus sylvestris* transect 3 invertebrate diversity (Simpson's index) data (m²), showing high contrast between 80 and 90 metre samples.
After which point mean density increases considerably and continues into the core of the habitat.

Two clear responses to core are seen in the SED plots of *P. sylvestris* combined (Figure 3.50) and transect 3 (Figure 3.51) for total invertebrate diversity. The plot of the combined SED values for invertebrate diversity (Figure 3.50) shows some level of contrast throughout its length but a very extreme increase towards the core area, after 75 metres. This is associated with a rapid increase in the diversity scores of these samples. The SED plot is highlighting a rapid change in invertebrate diversity after 80 metres into *P. sylvestris* plantations; a result supported by the t-test findings of significantly higher diversity in the core area (Table 3.4).

A similar pattern is seen in the individual plot of SEDs in *Pinus sylvestris* transect 3 (Figure 3.51). SED contrast increases rapidly towards the core area of the transect, again associated with increased diversity values towards the core. This again supports the conclusion that invertebrate diversity is higher in the core areas of *P. sylvestris* plantations. Overall SED and RED plots have been useful in defining some key depths of edge-effects for some invertebrates and in particular for abiotic conditions. Abiotic data show repeated and clear patterns responding to plantation edge which SED analysis highlights well. Invertebrate data has a tendency to be more variable, leading to more random noise in the SED and RED plots making the number of clear edge-effect results low.
3.4 Discussion.

Clear edge-effects are discernible in the plantation patches of *P. sitchensis* and *P. sylvestris* under investigation, a response to the presence of forest extraction tracks. Both positive and negative edge-effects occur in the abiotic and biotic data, with invertebrates showing responses at the ordinal, family and species level. The presence of these edge-effects supports the findings of previous research in similar UK plantations (Ozanne 1991), as well as the general occurrence of edge-effects reported in forest habitats around the world (Lovejoy *et al.* 1986, Andren and Angelstam 1988, Chen *et al.* 1993, Baldi and Kisbenedek 1994, Camargo and Kapos 1995, Peltonen *et al.* 1997).

The present data set follows the edge-effect response beyond the 50 metre depth previously researched in UK plantations, to a depth of 100 metres, highlighting the pattern in temperature (°C), relative humidity (%) and the invertebrate community changes to this greater depth. As well as different responses in the abiotic data and various aspects of the invertebrate community, clear differences are seen in the overall edge-effect trend between the two tree species. The invertebrate community of *P. sitchensis* shows more positive responses to edge proximity than that of *P. sylvestris*, with more invertebrate species showing increased densities or species richness at the edge of plantations than in the core. Whilst the invertebrate communities in *P. sylvestris* seem to respond negatively to edge proximity with densities and species richness more commonly higher in the core area. Guild analysis follows a similar pattern with guilds
responding positively to edge proximity in *P. sitchensis* but not *P. sylvestris*, which shows a single negative response to edge in the Acarina guilds.

### 3.4.1 Abiotic Edge-Effects.

Relative humidity (%) and temperature (°C) show clear edge-effects in both species, but of a particularly regular nature in *Picea sitchensis*. The smoothness of the abiotic responses seen in *P. sitchensis* is a result of uniformity in the canopy, with branches occurring close to the ground reducing through-wind at the trunk level (Mitchell 1985, Savill and Evans 1986). As expected, humidity increased and temperature decreased with distance from plantation edge in this species, with the most extreme differences seen over the first 5 metres (Figures 3.1-3.5). Although the main variation occurs over these first few metres, in many cases readings do not appear to stabilise until a greater depth of some 30 metres. Statistical analysis of the gross edge and core data supports the proposal of higher humidity and low temperature in the core areas of these plantations (Tables 3.1 and 3.2), humidity being 5 to 6% higher and temperature on average 1°C lower in the core areas.

*Pinus sylvestris* transects follow these patterns in abiotic data for most of the transects although in general abiotic readings are more variable, with significance less likely to be achieved in the analysis. This variation was caused by the more open growth nature of the tree species with fewer lower branches and foliage and greater inter trunk space (Mitchell 1985, Savill and Evans 1986), resulting in more sun spots and through-winds making
readings more variable. Relative to *P. sitchensis*, the *P. sylvestris* plantation patches had lower humidity readings and higher temperatures, however, as the samples were taken on different days and years no overall conclusions can be draw from this trend. Although the data are more variable a similar pattern of approximately 5% increase in humidity and 1°C reduction in temperature occurs in *P. sylvestris* plantations.

The combination of both relative humidity (%) and temperature (°C) data in the squared euclidean distance (SED) analysis supports these findings of higher core humidity and lower temperature (Figures 3.39-3.43). The method attempts to define the point of highest contrast in the data, a position considered to define the point of interface between two communities or areas of specific conditions. In the relatively stable habitat of *P. sitchensis* the average SED depth is 5 metres, highlighting the highest point of contrast but failing to provide a realistic estimation of edge-effect depths, likely to be closer to 30 metres where more subtle variations are seen. The SED plots in *P. sylvestris* are more variable due to the open canopy with high SED and therefore high inter-sample variation values over the first 30 metres, closer to that of visual estimation.

For these plantations in both tree species it appears that there is a rapid change in abiotic conditions within 5 metres of the forest tracks (edges), with temperature decreasing and humidity increasing with distance from the edge, this change continues amongst the canopy for a further 25 metres before conditions appear to stabilise, 5% more humid and 1°C cooler than the edge. This quantity of change in the abiotic conditions is similar to those found in previous studies, with differences of 1°C and 5% relative humidity
reported across edges of Douglas-fir forests in the Pacific Northwest of North America (Chen et al. 1993).

These changes in abiotic conditions are more than enough to have a biological effect on the invertebrate community in the canopy, as invertebrates are affected by relatively small changes in abiotic conditions, resulting in changes in development and behaviour (Speight and Wainhouse 1989). Rapid increases can occur in some invertebrate populations with slight changes in climate resulting in pest outbreaks (Speight and Wainhouse 1989, Royama 1997), and with expected global warming of 2°C likely to encourage large populations of herbivorous insects in Britain (Docherty et al. 1997). Humidity is a particularly important factor for some small invertebrates such as the Collembola whose longevity have been reported to be reduced in dry atmospheres (Lambert 1970), the animals actively migrating through the canopy or soil layer following ideal moisture conditions (Hopkin 1997). Likewise, temperature has a considerable effect on canopy Collembola; the invertebrates in general preferring lower rather than higher temperatures (Aitchison 1983). Therefore the variation in abiotic conditions across the edges of these conifer plantations will be affecting the invertebrate community captured in the different areas. Those larger invertebrates more capable of maintaining homeostasis, such as the herbivores or beetles, more likely to be found in the warmer edge habitat, whilst small organisms more dependent on microclimate will prefer the cooler moister conditions in the core.
3.4.2 General Invertebrate Edge-Effects.

Invertebrate responses to edge proximity differ considerably between tree species, with positive responses to edge, i.e. higher densities, species richness or diversities, in *P. sitchensis*, and negative responses to edge conditions, demonstrated by increased densities and diversities in core areas, predominantly in *P. sylvestris*. Six orders of invertebrates show the bulk of responses to either edge or core habitats in the two tree species, the Acarina, Araneae, Coleoptera, Collembola, Diptera and Hemiptera, leaving just a few significant results for total invertebrates and the Neuroptera. Many of these orders have been shown to respond to edge proximity in previous research (Ozanne 1991, Baldi and Kisbenedek 1994, Didham 1997, Ozanne *et al*. 1997), with the Acarina, Araneae and Collembola being particularly sensitive invertebrates to changes in habitat structure and climate (Lambert 1970, Bowden *et al*. 1976, Gunnarsson 1988, Hopkin 1998, Walter and Behan-Pelletier 1999).

The complete invertebrate community shows no significant variations in densities between the edge and core habitats in either tree species, however differences are seen in order-level species richness and diversity. It appears that throughout the canopies of both tree species similar invertebrate densities occur per m² ground area, however the communities are comprised of different invertebrate species in the edge and core habitats of the canopies (see below). Both richness and diversity are higher in the edge region of *P. sitchensis* whilst species diversity is higher in the core area of *P. sylvestris* (Table 3.5).
The *P. sitchensis* plantation as a whole has a relatively simple invertebrate community (Chapter 5) except for the edge zone which is particularly diverse in Coleoptera and Acarina. In contrast *P. sylvestris* shows a rich invertebrate community that is particularly diverse in the core area of the plantations, with in general more Acarina species in the core. Therefore richness patterns are following very different forms in the two tree species with the warmer, less humid and heavily foliated edge area of *P. sitchensis* encouraging high invertebrate richness, whilst the cooler more humid core area of the native *P. sylvestris* encourages higher diversity. This highlights a fundamental difference in the response of invertebrates to edge proximity in the two tree species, which in turn will influence the importance of core habitat in the two species (Chapter 4). The presence of core habitat is important in achieving high invertebrate diversity in native *P. sylvestris* plantations, making the issue of patch size vital in the management of this tree species, especially the maintenance of large enough patches to support core habitat and its diverse invertebrate community. In contrast it appears that the presence of edge habitat is vital in encouraging species richness in *P. sitchensis* plantations.

These patterns of response to either the edge and core habitats in the two tree species are followed by the guild analysis. In general the analysis of the guild composition of the total invertebrate community between the edge and core areas in the two tree species resulted in few significant results and no patterns in the predator/prey ratios. Just two invertebrate guilds, the scavengers and herbivores, show higher densities in the edge of *P. sitchensis* transects (Table 3.6). Increased scavenger densities being mainly accounted for by the Diptera found in higher densities in the edge (see below) and other orders such as
the Thysanoptera and Dermaptera utilising the canopy from the adjoining habitats. Increased densities of Herbivores in the edge is a result solely of the high numbers of Hemiptera in the edge habitat, present due to improved food availability in the edge zone (see below).

A surprisingly negative result is the lack of pattern in the predatory/prey ratios between the edge and core samples or with distance from edge. Previous research in an UK conifer species found elevated predator/prey ratios over the first 21 metres from plantation edge, although predator densities were not higher at the edge (Ozanne et al. 1997). This suggests that increased predation may be an important factor in the edge habitat, which has been supported for other organisms, predation rates of bird nests being higher in edge habitat (Wilcove 1985, Andren and Angelstam 1988, Burkey 1993). The lack of higher predator/prey ratios in the edge here, suggests that prey are under similar pressure throughout the plantations, edge proximity having little effect on this functional aspect of the invertebrate community. However this may not be the case as differences in predator densities and species richness at the ordinal level show variation with distance from plantation edge (see below). The response therefore may not be at the community level but more at species level with specific predators being higher in the edge habitat increasing the predator pressure on their specific prey items.

The plots of guild densities with distance from edge show few patterns, with in general inter-sample variation of the guild densities being high. This is unsurprising as the guild density data would follow the pattern of the highly variable densities of invertebrates,
however it would be expected that the relative proportions of the guilds would be similar between samples, due to the functional constancy of guilds (Moran and Southwood 1982, Stork 1987a, Hawkins and MacMahon 1989). This is the case, with few major differences between the percentage contribution made by each guild in the two habitat types. Just one guild shows any pattern in its densities with distance from edge the tourists appearing to show higher densities in the edge (Figure 3.23). Increased numbers of tourists would be expected, as transient species are more likely to occur in the edge habitat close to adjacent habitat types. Interestingly a similar pattern of increased tourist is not seen in the edge of P. sylvestris (Figure 3.24), which shows higher densities and high variation between samples throughout the length of the transect, highlighting the species’ more diverse community throughout the plantation.

3.4.3 Coleopteran Edge-Effects.

Coleoptera show the most marked response to edge proximity in P. sitchensis plantations, yielding both increased densities per m² ground area (Figures 3.10) and increased species richness in the edge (Figure 3.12), along with differences in guild densities and species richness (Table 3.7 and Figure 3.27). Most of the density data can be attributed to one family the Coccinellidae, which occur in higher numbers in the edge samples, particularly Aphidecta obliterata (Figure 3.11), a species commonly associated with fir trees. These increased numbers of predatory beetles in the edge samples are likely to be a response to increased densities of potential prey in the edge, particularly the Hemiptera which also show higher densities in the edge samples (Figure 3.15). The Coleoptera predatory guild
also shows higher densities in the edge samples, again a reflection of the higher densities of Coccinellidae.

Other studies have found both increased (Helle and Muona 1985, Greatorex-Davies et al. 1994) and decreased abundances of Coleoptera in edge habitats (Ozanne et al. 1997). Increased densities have been related to increased prey availability and reduced shading in the edge habitat (Greatorex-Davies et al. 1994), reduced shading encouraging ground species and those of open habitats such as the Coccinellidae. The high densities of Hemiptera are a response to increased food abundance in the edge habitat, with increased lateral growth and greening of the trees at the very edge of forest plantations (Forman and Godron 1986, Lovejoy et al. 1986, Williams-Linera 1990, Chen et al. 1992). Coleoptera density also reflects a definable edge-effect of 2.5 metres (Figure 3.45) in its relative euclidean distance analysis, so coleopteran densities are especially high over the first 5 metres of *P. sitchensis* plantations.

Increased species richness of the Coleoptera in the edge area of *P. sitchensis* is caused by the presence of just three families. The core samples contain a simple community of Coccinellidae, predominantly *Aphidecta obliterata*, however the edge samples also contain Carabidae, Curculionidae and Lathridiidae. Increased occurrence of Carabids in the edge samples has previously been reported (Bedford and Usher 1994). The order are active hunters in open areas, often with increased species richness and abundance in open areas or small forest fragments, representing mostly edge habitat (Halme and Niemela 1993). Increased occurrence in the edge samples is likely to result in overlap of the
grassland species into the first few metres of the forest (Bedford and Usher 1994), the family being capable of accessing the canopy habitat to hunt. Curculionidae could also be responding to the increased greening and therefore food source in the edge samples, as they are herbivores, the herbivorous guild showing higher densities in the edge samples. More weevil species have been found in less-shaded, edge habitats (Greatorex-Davies et al. 1994). An increase in species richness within the herbivorous guild is seen in the edge samples, a possible reflection of this association with the food sources in the edge. Although the family shows a different response in *P. sylvestris* in other research with higher species richness in core areas (Ozanne 1991). The Lathridiidae are a predominantly scavenging fungi eating species, with the higher quantity of standing dead organic matter in the core area of *P. sitchensis* plantation providing increased food sources. Although the Coleoptera show no significant differences in the *P. sylvestris* data set, the guild structure of the Coleoptera does appear to show an edge response in this tree species. Both the detritivore and predatory guilds contributing more to the coleopteran community in the edge samples compared to the core (Figure 3.28). Again the higher contribution of predation could be a fusion of the two communities at the edge however detritivores should be more abundant in core habitats where increased standing dead organic matter is found.

3.4.4 Dipteran Edge-Effects.

Diptera show increased densities per m² in the edge habitat of *Picea sitchensis*, although no variation was seen in their richness. The Diptera were mostly adult and are considered
tourists or scavengers in the canopy (Moran and Southwood 1982, Stork 1991, Didham 1997). Although many dipteran adults do not associate directly with trees, they have shown clumped distributions within forest canopies (Didham 1997), suggesting a response to some aspect of the canopy, potentially making them a more important group in the community than their ‘tourist’ designation may suggest. Increased dipteran densities have been associated with canopy cover, higher densities occurring in more open sites (Didham 1997), therefore higher densities should be expected in edge habitats. Distance from forest edge also acts as a predictor for species richness and diversity in the Diptera with increased richness near forest edges (Didham 1997), these two factors explaining variations in dipteran community above all other structural aspects of the tree canopy. It therefore appears that the dipteran community in _P. sitchensis_ is being encouraged by the proximity of the forest edge and the ease of access to open flight paths it provides. Whereas the more generally open canopy of _P. sylvestris_ provides suitable open canopy throughout its area leading to equal densities of Diptera in both edge and core areas.

3.4.5 Araneae Edge-Effects.

Varying responses to edge proximity have been reported for the Araneae, with ground species reported to prefer edge habitats (Bedford and Usher 1994), resulting from increased structural complexity at the edge due to understory complexity and the fusion of two communities. However canopy studies in plantations have reported a tendency for increased densities and species richness in interior regions of plantations (Ozanne 1991,
Ozanne et al. 1997), a response especially apparent in woodland specialist species. The finding here of increased Linyphiidae densities in the edge samples of *P. sitchensis* opposes previous findings as the majority of Linyphiidae in this case predominantly the genus *Lepthyphantes*, are considered to be woodland specialist species. The edge habitat of *P. sitchensis* must be providing specific structural complexity required by the genus. However the significant results from the *P. sylvestris* plantations follow the expected pattern. Two species of Araneae, both considered woodland specialists have increased densities in core areas. The first, *Drapetisca socialis*, is a widespread species in the UK associated with tree bark, building its webs between the ridges in bark (Roberts 1987); its presence in the stable core habitat is therefore unsurprising. The second, *Lepthyphantes expunctus* is a common species found on pines in Scotland and Northern England, although most commonly recorded from the edge of woodland habitats amongst small clearings and near paths (Roberts 1987); here it is more common in the core samples.

3.4.6 Collembolan Edge-Effects.

*Sminthurus fuscus* (Collembola) show increased density in the edge habitat of *P. sitchensis* (Figure 3.19), this opposes the overall finding of increased Collembolan density in the core areas of the plantations (Figures 3.17). *Entomobrya nivalis* is particularly abundant in the core area (Figure 3.29) it is a widespread species but has been shown to have a slight preference for wooded areas over open habitats (Bowden et al. 1976). Such increased density in the core area is expected due to the more stable environmental conditions leading to an increased likelihood of lichens, algae and fungi.
growing in the area (Esseen et al. 1996). Epiphytic lichen biomass is higher in old growth forest, a result of stable conditions and the increased length of growing time (Pettersson et al. 1995, Esseen et al. 1996). Corticolus lichens and algae densities have been found to correlate consistently with collembolan density, suggesting they are a primary food source for these invertebrates (Bowden et al. 1976, Stubbs 1989 and Pettersson et al. 1995). In fact stratification in invertebrate populations of epiphytes can occur in a single tree with very specific communities associating with microhabitats of different types of epiphyte (Andre 1985, Rodgers and Kitching 1998). The occurrence of *Sminthurus fuscus* in the edge habitat is unusual as this species is deterred from bright dry areas, over and above that of other species including *E. nivalis* (Bowden et al. 1976). This is highlighted by the lack of *S. fuscus* caught in light traps, although the species was present in the adjacent habitat (Bowden et al. 1976). It would be expected therefore that the species would not show higher densities in the dryer and warmer habitat of plantation edge, the environmental conditions cannot be so extreme that *S. fuscus* is deterred from the area and other factors such as specific food supply must be encouraging their presence in the edge region.

The pattern of increased collembolan density is repeated in the *Pinus sylvestris* core samples, again predominantly *E. nivalis* (Figures 3.31 and 3.32). Densities are considerably higher in the core with means over a hundred compared to just ten or so in the edge samples. Collembolan density also shows a clear core effect in its relative euclidean distance plot (Figure 3.50) for this tree species. Collembola are responding clearly to edge proximity within both tree species studied generally showing a negative
response with increased densities in core areas, most likely to be associated with increased lichen supplies in these areas and the more humid conditions present preferred by the dry intolerant species. Collembola are important organisms in soil ecosystems aiding litter decomposition and soil formation (Takeda and Ichimura 1983, Hopkin 1998), however their function in the canopy is less clear, although the role is likely to be similar especially in canopy soils, important sites for other small invertebrates such as the Acarina (Winchester and Ring 1996, Winchester 1997b). If the Collembola perform a similar function in the canopy then their loss from certain areas due to edge-effects may lead to reduction in through canopy nutrient cycling within that region and a reduction in potential plant performance, reducing habitat quality. In this instance reduction of edge-effects may need to be encouraged to maintain effective nutrient cycling systems within the habitat.

3.4.7 Acarina Edge-Effects.

Acarina are considered an important and under-investigated aspect of the canopy community (Walter and O'Dowd 1995, Winchester and Ring 1996, Walter and Behan-Pelletier 1999), a result of their small size, diversity and lack of taxonomic knowledge. Like the Collembola they are particularly responsive to structural complexity, microclimate and epiphyte cover (Stubbs 1989, Walter and Behan-Pelletier 1999), they may therefore be expected to respond to edge proximity in a similar way, although little study has been performed on their edge-effects. However unlike the Collembola they show no density edge-effect in P. sitchensis although their species richness is higher in
the edge samples, with a mean of approximately five species in the edge compared to three in the core. The extra species reported in the edge samples vary, being a few individuals from rare species, the edge habitat providing suitable conditions for these species. The collembolan guild structure also shows increased species richness in the edge samples in both the detritivore and predatory guilds, showing an across the board increase in species richness in the edge not just in one aspect of the guild.

Acarina follow a more expected pattern in *Pinus sylvestris*, with both increased density, and species richness and diversity in the core samples, responding to the diverse microhabitats available in stable habitats. The higher densities are mainly accounted for by the predatory guild (Figure 3.37) whilst the higher species richness is due to the detritivores. As well as total density of Acarina, three species respond to core conditions, *Anystis sp.* (Prostigmata), *Chamobates sp.* (Oribatida) and *Cymbaeremaus sp.* (Oribatida). *Anystis sp.* is generally an abundant species throughout the samples of both tree species with densities in the hundreds in some *Picea sitchensis* samples. These are predatory mites responding to diverse and abundant prey communities in the core habitat. *Chamobates sp.* which occurs in relatively low densities in the samples is significantly denser in the core areas, with three or four individuals per m$^2$ ground area (Table 3.3) this is a canopy species (Wallwork 1976) capable of living in many climatic conditions. *Acarina Cymbaeremaus sp.* shows considerably higher densities in the core samples (Table 3.4), this canopy species is particularly responding to the core habitat.
3.4.8 Conclusions.

Two clear patterns seem to be appearing in the invertebrate responses to edge-effects in the plantation communities. It is apparent that invertebrates respond differently to edge proximity depending on their life-style requirements, and that the invertebrate communities of the two tree species respond in very different ways. Invertebrates such as the Coleoptera, Diptera and Hemiptera are responding positively to edge proximity with higher densities and in the case of Coleoptera richness, responding to the structural complexity and specific food sources available in the region, with edge-effect depths of 5 metres for RED analysis and up to 30 metres for visual assessment. However the smaller fungivore/detritivore invertebrates such as the Collembola and Acarina show negative responses to edge proximity with increased densities in the core habitat again responding to food source availability and microclimate stability. These organisms are showing edge-effect depths up to 80 metres with populations becoming more abundant after this distance from the edge. The invertebrate communities as a whole respond to edge proximity in very different ways between the two tree species under investigation, with higher richness recorded in the edge habitat of *P. sitchensis* whilst the core area of *P. sylvestris* supports the most diverse invertebrate community. It appears that two distinct communities occur in the edge and core habitats of the two tree species. A predator-dominated community of relatively large invertebrates is located in the edge area of *Picea sitchensis*, with high densities of Coleoptera and Linyphiidae. Whereas in the core areas of *Pinus sylvestris* a community of detritivores is developing, centred on large numbers of Acarina and Collembola at both the order and species level. The same core
habitat is also an important reserve for specific woodland specialist species particularly examples of spiders (*Drapetisca socialis, Lepthyphantes expunctus*).

These differences mean the same plantation management will have very different effects on the invertebrate communities of the two tree species, and highlight the fact that management based on a single invertebrate species would be inappropriate. Management of *P. sitchensis* plantations to encourage Coleoptera, which would lead to an increase in edge habitat, would generally increase the richness of the invertebrate community but to the detriment of the core collembolan community, which may play an important nutrient cycling function. However the same increase in edge zone in a *P. sylvestris* plantation would lead to an overall loss of invertebrate diversity due to the loss of core habitat, the site of highest diversity. Therefore management activities within UK conifer plantations need to be considered carefully with due reference to the complete invertebrate community and the tree species under investigation to establish the best possible method of encouraging high invertebrate diversities, if indeed that is the conservation aim.
Chapter 4. Core-Area Models.

4.1 Introduction.

In the previous chapter we elucidated the depth of edge-effects in the invertebrates of conifer plantations, finding different species and communities preferring edge and core habitats. A number of invertebrates show very different densities and diversities in the edge and core habitats (Chapter 3), particularly key woodland specialist species occurring in the core areas alone, i.e. Drapetisca socialis (Araneae). Core-area models calculated in this chapter enable the assessment of the proportion of a patch under edge and core conditions and therefore the quantity of the patch available to species occupying one or other of the habitats. From this data calculation of the minimum patch size capable of providing core habitat is possible. Core-area models, developed out of the concept of the species area relationship, calculate the quantity of core habitat in any given patch size for any given edge-effect depth using information on patch size, perimeter length and shape index (Patton 1975). To date, core-area models have been used predominantly on hypothetical data, the further use of the model here with field data helps to ascertain their usefulness as a tool in habitat management and the monitoring of species diversity. Core-area models can also be used to assess the affects of edge management on core area size, and the potential effects on the invertebrate communities in these areas. Plantation edge management, including the removal of areas of trees, resulting in convoluted plantation edges and increased area of grassy rides, encourages invertebrates common in the edge habitat, especially the Lepidoptera (Greatorex-Davies 1991). However the effects of this
management on the canopy invertebrate communities have not been assessed. Scalloping of edges may reduce plantation core area, potentially leading to a loss of the habitat capable of supporting woodland specialist species. Re-calculation of plantation patch size under these management techniques using the edge-effect depths obtained in Chapter 3 will show the specific effects implementation of these methods would have on the proportion of edge and core habitats in conifer plantations.

Core-area models use a combination of information about the size and shape of plantation patches to calculate proportions of edge and core habitat. However this combination of data was not always used as the method of assessing the effects of habitat patch size on species richness. Previously patch size or shape alone were used before being integrated into a more explanatory model.

4.1.1 Patch Size.

For many years, area per se was considered the most important issue in encouraging species richness in nature reserves or specific habitat patches such as plantations, this was a reflection of the dominance of the species area concept in ecological theory during the 1970s. The largest habitat areas possible were considered preferable, as extinction rates are minimised (Diamond 1975), however there are limitations to considering patches in the light of size alone. Large patches may fail to encompass the maximum number of species or fail to encompass the prime habitat of key conservation species (Blake and Karr 1984). Therefore small areas of habitat specifically encompassing key habitats may be of more use (Usher et al. 1992, Turner
and Corlett 1996). A debate developed in the mid-nineteen seventies as to whether single large or several small reserves were more likely to support species-rich communities, this was coined the SLOSS debate (e.g., Diamond 1975, Wilson and Willis 1975, Diamond and May 1976, Simberloff and Abele 1982, Blake and Karr 1984, Kupfer 1995). The selection of either one large or several small patches must be considered with the conservation aim in mind as the minimisation of extinction rates is achieved with large reserves whilst the coverage of many species (habitats) is achieved with a number of small reserves (Muhlenberg et al. 1991).

The species-area relationship suggests that all reserves should be of a larger size if species richness alone is the conservation aim. Indeed large areas are important to some species, for example, a clear area effect was found in the Bay checkerspot butterfly population of California. A large persistent population occurred in large habitat patches compared to unstable populations with continual turnover, in smaller habitat patches (Harrison et al. 1988). High species number in large areas is however not always the case; using the simple form of the species-area relationship \( S = cA^2 \) Simberloff and Abele (1976) compared the number of species in a large reserve with those occurring in two reserves of the same total area. For a wide range of species the analysis showed that there was no consistent difference in species richness between a single large site and several small sites combined, and that several small sites had a greater combined species richness (Simberloff and Abele 1976). Similar results were found for mammals on isolated mountaintops, where the number of species expected in one large or a number of smaller areas was the same, although the species present differed (Taylor 1991). The most likely explanation proposed for this result was that
two or more reserves are likely to encompass a greater variety of habitats if they are further apart, than the area that would be encompassed by a single large reserve, resulting in increased species richness.

Smaller habitat patches may have higher species richness than larger patches in some instances, but smaller habitat areas also have limitations. The increase in species richness seen in smaller reserves is reversed at a critical point by a disproportionate increase in extinction rates, due to external processes both natural and anthropogenic dominating the area (Janzen 1983). The area can also drop below that which is able to support minimum viable populations (Muhlenberg et al. 1991). Andren (1994) found that species of birds and mammals were capable of maintaining populations in landscapes with 30% of the original habitat, whereas, below this, (10-30%), rapid species loss was encountered, and exponential increase in distance between patches was seen. More disturbance-sensitive species or those requiring large home ranges had their populations seriously affected below 60-70% of original habitat (Andren 1994). Greater predation rates often occur in edge habitat, in excessively small reserves, leading to reduced species richness (Blake and Karr 1987, Andren and Angelstam 1988).

It is therefore apparent that considering size alone when designing nature reserves in heterogeneous habitats is inappropriate, as both large and small reserves provide different species with habitat. Small reserves act as stepping stones for species dispersal throughout the matrix, sometimes supporting high species densities and high population sizes of edge species, and protect scattered small habitats and rare species
Whereas large areas of habitat provide protected areas for those species with large home ranges, and encompass a selection of habitat types. It is therefore inappropriate to argue solely for either large or small nature reserves, but to attempt a more encompassing system of both large and small reserves within a landscape, each playing a vital role in increasing species richness.

The concept of a number of mixed sizes of habitat patches may be less of a consideration when dealing with homogenous habitats such as managed systems in plantation forestry, as diversity of habitats is less of an issue. Here the habitat is often being maintained in an early successional state with the early pioneer species held in a monoculture and felled regularly. Other than the effects of edge disturbance (Chapter 3) the system is reasonably uniform, it can be envisaged that beyond a certain size no new species would be accrued due to any increase in habitat types present. Therefore the issue in managed systems may be to achieve a minimum habitat size that contains enough core forest habitat to support specialist species, rather than concentrating on total patch area.

4.1.2 Patch Shape.

Area can be an important issue in the design and implementation of nature reserves but is less so when considering managed habitats, however shape is a factor that affects species richness in both nature reserves and managed systems (Game 1980, Blouin and Connor 1985). Although studies of patch shape have proliferated it has been contended that shape indices add nothing to predicting species richness patterns,
with studies showing that, after controlling for area no correlation is found between island shape and species richness (Blouin and Connor 1985, Usher et al. 1992), suggesting that area or indeed other factors are more important. If however shape is important and affects species richness it may be due to two reasons:

(1) Reserves with highly convoluted shapes may be more susceptible to stress or disturbances originating outside the patch because a proportionately greater amount of the reserve area is exposed to the exterior habitat and

(2) Irregularly shaped patches have a proportionately greater amount of edge area in proportion to core area (Kupfer 1995) reducing potential habitat for some species.

These factors have resulted in the development of two types of model attempting to explain the situations seen in reserves or habitat patches of varying shape. Shape models (1) attempt to account for the effects solely due to patch shape, whilst core-area models (2) consider the proportional differences between edge and core areas and how these might predict the ability of a habitat patch to support a representative, species rich community, of that habitat type.

Patch shape is a rich concept due to the complexity and variety of shapes possible within a landscape (Forman 1995). In theory compact forms (i.e. circles) are effective in conserving resources by protecting internal areas against detrimental external effects, such as livestock grazing, poaching or increased competition from neighbouring habitat species. Assuming substrate or habitat homogeneity, a compact patch should contain higher species richness than an elongated patch with its fewer
interior species (Temple 1986), because increasing interior area adds species at a
greater rate than increasing edge area (Forman 1981). But this may be balanced by
the fact that convoluted or elongated patches are more efficient at sampling natural
communities when compared to circular plots, by including more habitat
heterogeneity, which leads to increased species diversity. Convoluted boundaries also
enhance interactions with the surrounding habitats, which can be both positive and
negative; a blending of the species of the two habitats is often seen, increasing
diversity and potential competition. Some area-related extinction may in fact be a
result of these edge processes, for example some bird species reliant on core habitat
are absent from small deciduous forest patches (Temple 1986). Two reserves of the
same area and isolation but varying in shape could exhibit differences in species
number and composition because of their differing exposure to edge conditions
(Schonewald-Cox and Bayless 1986), the more convoluted patch having a lower
species number due to the loss of core specialist species (Temple 1986). Convoluted
patches are also more likely to suffer from the peninsular effect (Forman and Godron
1986). Diamond (1975) suggests that dispersal rates from reserve cores to outlying
areas may be low in irregularly shaped reserves, due to a concentration of unsuitable
habitat in the lobe or increased distance from source pool (core population),
increasing the possibility of island-like extinctions.

It can be seen that there is lack of clarity as to which of these two habitat forms,
convoluted or compact, is of greatest use in the achievement of high species richness.
Game (1980) argued that convoluted reserves may have both higher and lower
immigration rates and that an optimal shape will be a balance between the two. There
is a fundamental problem however with attempting to link reserve shape effects with species richness; habitat patches with convoluted shapes may be primarily composed of edge species while more circular patches contain a large number of rare interior species. Thus patches of different shapes might possess similar species richness values but different species assemblages, especially important in small reserves where a small deviation from circularity can drastically decrease the amount of interior habitat. Therefore the shape of reserve chosen specifically relates to the species that is to be conserved. If full species richness of both edge and core species is desirable, then the patch can be convoluted to encourage edge species but must be large enough to encompass the minimum quantity of core area.

4.1.3 Size and Shape Models.

Several researchers have suggested the use of geometric indices incorporating patch size and shape to derive a measure of the complexity of the patch shape (Kupfer 1995). The most commonly cited examples are the perimeter-area ratio and its more complex relative the shape index (SI) (Patton 1975, Game 1980). More than a dozen indices have been developed that use area and/or perimeter measurements to indicate how much a shape deviates from circularity, but none are able to highlight whether the deviation from circularity is due to elongation, convolution, roughness, or some combination thereof.

Some simple models of shape are based on geometric-figure fitting (Forman 1995), where the largest rectangle or circle is added to the area, thus excluding lobes and
convolutions in comparing the size of patches, hence focusing on the core of the habitat area. Two patches of the same area but different shapes would support different sized geometric-figures (i.e. circles or squares) in their cores, the more evenly shaped patch supporting a larger shape than one which is more convoluted. Rectangles are common in the landscape, tending to have an average length to width ratio (L: W) of 1.5:1 to 4:1 (Forman 1995), and have been used as a common figure to fit to habitat patches, however this length/width ratio only measures elongation (E = w/l). The use of the largest circle gives more idea of the core area, excluding lobes, and this may have value when considering the home ranges of interior loving species, such ranges particularly of mammals often being circular or ovoid (Covich 1976).

Circularity (C) can be measured in a number of ways based upon:

1. Lengths of axes (Davis 1986): \[ C_1 = \frac{lw}{\ell^2} \]
2. Area (Unwin 1981, Davis 1986): \[ C_2 = \frac{A}{Ac} \]
3. Perimeter and area (Davis 1986): \[ C_3 = \frac{4A}{p^2} \]

Where \( A \) = area of patch, \( Ac \) = area of smallest circle enclosing a patch, \( l \) = length of long axis, \( p \) = perimeter of patch, \( R_j \) = \( j \)th radius of patch, measured from centroid to margin and \( w \) = width of patch perpendicular to long axis.

Another method of using the circular theory is that of the mean radius (\( R = \frac{R_j}{n} \)),

151
which attempts to calculate the core area of a patch from the radius of the largest circle capable of being drawn in the patch. However this fails to work with some convoluted shapes, where, due to large indentations into the core only a very small circle can be achieved resulting in a small radius figure which bears no relation to the true area of the habitat patch. These models are giving very basic information on the largest single shape possible in a habitat fragment, which can be used only to compare patches in a very relative way.

One of the more common models used to consider impact of external influence is the perimeter/area model (Diamond 1976, Diamond and May 1976, Forman and Godron 1986, Schonewald-Cox and Bayless 1986). This accurately incorporates both size and shape variation of fragments by using the perimeter length to area (p/a) ratio as a measure of the principal exposure of the reserve's interior to the exterior. If the p/a ratio is low for a reserve (e.g. bar-shaped), the average distance from any interior point to the nearest edge is small, in such cases, external processes i.e. increased predation, have a strong influence on internal species. If the p/a ratio is high for a reserve (e.g. circular) of the same size, the average distance from any point to the edge is increased, and exposure is decreased. The extent of the influence of the exterior on the interior is defined as the exposure of the reserve (Schonewald-Cox and Bayless 1986); and exposure is a major determinant of the extinction probability of species. Therefore boundary effects will be less on internal processes of extremely large reserves, but much stronger on the processes of smaller reserves.

If reserves are the same size but of varying shapes, the boundary model suggests that
those with smaller p/a ratios will experience a greater impact from edge species and internal changes. Indeed perimeter length was found to be a better predictor of avian richness than total area in suburban woods (Gotfryd and Hansell 1986). This supports once again that large reserves are more beneficial for supporting specific interior species than highly exposed small reserves, contradicting Simberloff and Abele's (1982) work.

4.1.4 Core-Area Models.

It has been argued that perimeter-area ratios can yield sizeable errors (> 20%) when used to estimate the amount of edge and core areas in forest fragments of different shapes, thereby leading to inaccurate conclusions about reserve functioning (Laurance and Yensen 1991). Perimeter/area ratio represents an index of percentage core area, which has been found to be approximately linear with percentage core area (Laurance and Yensen 1991), however this linearity is reduced, as the shape becomes more circular. Also different shapes (i.e. circle and fernleaf) can, by adjusting their areas, be given the same p/a ratio even though the latter will lose core area more rapidly than the circle with increasing edge-effect depth (Laurance and Yensen 1991). Temple (1986) and Laurance and Yensen (1991) have advocated the use of a core-area model rather than a perimeter/area ratio or a species-area model to estimate species richness for a patch or reserve. The core-area model is a modification of the p/a ratio concept which incorporates the two dimensional nature of edges by including an edge depth. This edge depth, or edge-effect, is variable depending on species studied; the result is an estimate of edge and interior areas which can
theoretically be compared to the minimum area requirements of the species.

Edge-effects are the response of the biotic community to changes in conditions at the interface or edges between different habitats (Chapter 3). These effects reach into the habitat patch for varying distances depending on the species under investigation, resulting in a percentage of the fragment being reduced to a 'core' area smaller than the overall area of the reserve or patch. These different habitat types ('edge' and 'core') may not be favourable to all species resulting in changes in community structure. Edge-effects mean the effective reduction of the reserve area for some species. The concentration on percentage of core area rather than total patch area, changes the emphasis from the maintenance of high species richness in the whole patch to the preservation of specific habitat conditions (i.e. core conditions) required by specialist species. This is more closely related to conservation management, which often concentrates on the preservation of a key species within a habitat, with any improvement of total species richness a by-product of the specific management for the single species.

A number of researchers have used core-area models to assess the capacity of nature reserves of varying sizes to support certain species (Temple 1986, Laurance and Yensen 1991, Laurance 1991, Malcolm 1994). Temple (1986) compared a total area model with a core-area model (edge-effect 100m) to discover whether core area was a better predictor of bird abundance than total area. The core-area model was found to account for more of the variation in population estimates of species sensitive to fragmentation than total area. The core-area model was also considerably more
accurate at predicting the presence and absence of birds in fragments that had a large total area, but due to their shape had little or no core area (Temple 1986). So core area is a better general predictor of extinction of specific species, in this case birds, than total area and should therefore be the preferred model to use in the design of nature reserves for bird populations (Temple 1986). Specific assessment of the predictive ability of total versus core area has not been performed for invertebrate species, however invertebrates have been shown to respond to edge proximity in a similar way to birds (Ozanne et al. 1997, Peltonen et al. 1997). Therefore quantity of core habitat as predicted by the core-area model is also likely to be more successful in the prediction of the likely population of these invertebrates than the use of total area.

Temple's (1986) model used a blanket edge-effect depth (100m), based on an average depth from many studies. It is preferable however to incorporate empirical data for edge-effects directly into the model along with landscape features of the fragment. The core-area model developed by Laurance and Yensen (1991) allows this to be carried out, the model predicts the impact of edge-effects, using two quantitative edge parameters together with area and perimeter length, as well as estimating the pristine habitat within the fragment. The model can be used to predict the unaltered habitat preserved within any hypothetical fragment, thus providing an excellent tool for reserve management.

The Laurance and Yensen (1991) core-area model requires a number of pieces of information
(1) $d =$ the edge function in metres. This is the penetration distance of an edge-effect for a given species, usually obtained by transects running perpendicular to the edge (Chapter 3),

(2) $TA =$ the total area of the fragment in hectares.

(3) $P =$ perimeter length of the fragment in metres.

(4) $SI =$ the fragment shape index, adapted from Patton (1975) calculated using the total area ($TA$) of the fragment in hectares and the perimeter length ($P$) of the fragment in metres, by

$$SI = \frac{P}{200 [(\pi \ TA)^{0.5}]} \quad (4.1)$$

The shape index assesses the fragments' deviation from circularity, a perfect circle will have an SI of 1.0, all other shapes will have higher values.

With this information it is possible to assess the rate at which core area declines as the depth of the edge-effect ($d$) is increased. To do this Laurance and Yensen (1991) set a total area of 10,000 hectares for five hypothetical fragments. Core area decreased in a nearly linear way, so for a given area, as edge-effects penetrate further, core area decreases at a constant, shape-specific, rate. For example, a fragment of 10,000 ha might lose 3.55 ha for every 1m increase in $d$ (Laurance and Yensen 1991). A linear relationship is also seen when relating fragment shape and core area decline, fragments with more irregular shapes (high SI) accrue edge-effects more rapidly (Laurance and Yensen 1991) therefore losing core area. Total fragment area is also important to core area, large fragments lose more hectares as $d$ increases because, in
an absolute sense, they have a longer exposed edge than small fragments. This means that for the core-area model to be accurate for any size of fragment, it is necessary to know how much the shape-specific rate of core area loss (ha m\(^{-1}\) SI unit\(^{-1}\)) increases as fragment area increases (Laurance and Yensen 1991) i.e. the relationship between shape and area.

As stated, the slope of core loss for a 10,000 ha fragment is 3.55 ha m\(^{-1}\) SI unit\(^{-1}\), so the slope for any other size can be found by multiplying the constant 3.55 by (TA/10,000)\(^{0.5}\) (Laurance and Yensen 1991).

This led to the first true core-area model, where Core Area = TA - Affected Area (AA) where

\[
AA = \{ (3.55) (d) (SI) [(TA/10,000)^{0.5}] \} \tag{4.2}
\]

Laurance and Yensen (1991) tested their first model against some empirically determined data and found a consistent <10% underestimation of core area when the core area affected was >75% of total area, but up to a 70% error rate when core area was very small, particularly for more circular fragments. This underestimation is related to properties of different shapes, because the relationship between core area and \(d\) becomes curvilinear for more circular fragments when core area becomes small, but stays nearly linear for irregular shapes (Laurance and Yensen 1991). Therefore fragments with SI values less than 1.5 have substantial underestimates of core area. The affected area (AA) can be adjusted down to minimise these shape-induced errors to an average error of 0.48% and no more than 3.8% (Laurance and

157
Yensen (1991) by

\[ AA_{adj} = AA \left[ 1 - \left( 0.265 \frac{AA}{TA} \right) \right] \]  
\[ (SI)^{1.5} \]  

so the adjusted Core Area model is:

\[ \text{Core Area}_{adj} = TA - AA_{adj} \]  
\[ (4.4) \]

When dealing with natural heterogeneity in the depth of edge-effects \( (d) \) obtained from field data, rather than using a single derived \( d \) as in the example above, it is preferable to apply the core-area model three times (Laurance and Yensen 1991). By applying the model three times, once for the mean value of \( d \), and once each for the upper and lower 95% confidence limits, the range of core areas expected for the given biological data are obtained. This means the sampling strategy of ecological fieldwork is very important, proving replicated data so a mean \( d \) can be calculated along with its 95% confidence limits.

The core-area model emphasises the quantification of edge-effects and the extrapolation of the data to existing as well as hypothetical situations, this can be useful in the planning of future nature reserve size and shape as well as forest plantation patch size. Once the reason for the nature reserve has been established and the requirements of key species or habitats for conservation are assessed (not necessarily a simple process), it is possible to state the minimum total reserve area which would contain a core area capable of supporting the desired organisms.
Laurance (1991) suggested that >50% of the total area should be core area to maintain rainforest conditions, then, applying the core-area model with the 50% figure in mind, found that isolated rainforest reserves should exceed 2000-4000 hectares (depending on reserve shape) to ensure the survival of pristine tropical rainforest floras. This was argued using empirically measured data of plant species present, however the largest fragment surveyed was only 590 hectares in size, and the model extrapolated the data to give a hypothetical prediction of the core area (Laurance 1991). It is therefore possible to apply this analysis to the various depths of edge-effects found in UK forest plantations, to see if minimum sizes of core habitat, 50%, are being achieved to support invertebrate species of particular conservation interest in the specific patches.

As well as assessing the quantity of core habitat in the research patches under investigation, extension of the edge-effect data to management patches will be performed. A forestry practice on the increase in the UK in recent years has been the landscaping of forest patches to increase edge habitat, thought to increase species richness per se, the diversity of specific species, most notably the Lepidoptera (Greatorex-Davies 1991) and increase the aesthetic appeal of plantation forests. Various methods of edge landscaping have been proposed by the Institute of Terrestrial Ecology and the Forestry Commission (Ferris-Kaan 1991), including the cutting back of trees at the corners of plantations opening up rides at the intersections of forest tracks (box junctions) and the cutting of bays into the perimeter, resulting in indentations of grassed areas into the plantation (Figure 4.1). These activities result in a number of changes in the edge habitat with increased light intensities (Yallop and
Hohenkerk 1991) and herbaceous plant diversity particularly important for lepidopteran species (Anderson and Buckley 1991, Greatorex-Davies 1991). However these management practices have specific effects on the patch size and perimeter length, often decreasing area and increasing perimeter length, resulting in changes in the shape index of the patches, and therefore the quantities of edge and core habitat they contain. By applying the edge-effect depths calculated in Chapter 3 to the research patches which have undergone simulated edge management the effects of the management process on the quantity of core habitat can be assessed and the likely affects on core species explored. The present study has gathered quantitative data for both microclimate and invertebrate communities, which will enable further testing of the Laurance and Yensen (1991) core-area model with field data. Finally it will ascertain the depth of edge-effects in UK plantation forestry, calculate the core area size in both research and management patches, and allow the development of guidelines for patch sizes and management techniques most suitable for the support of key invertebrate species or communities sensitive to edge proximity.
Figure 4.1. Diagram representing plantation edge management for the encouragement of edge invertebrates (Carter 1991, Greatorex-Davies 1991), showing relative loss of plantation area (shaded area) and perimeter length. A. represents 10 and 20 metre Box junctions (Box 10 and Box 20) cut into the corners of forest patches. B. represents high densities of 10 x 30 metre Bays cut into plantation edges every 30 metres (Bay 1). C. represents low density 10 x 30 metre Bays (Bay 2) cut every 60 metres along plantation edges.
4.2 Methods.

4.2.1. Research Patches.

Depths of significant edge-effects calculated in Chapter 3 for temperature, relative humidity and invertebrate density and diversity, guild structure and squared and relative euclidean distances, were used to calculate the proportion of edge and core areas in the research patches studied, using the Laurance and Yensen (1991) core-area model (Equation 4.2).

For relative humidity and temperature, edge-effect depths were provided by the mean data from each tree species and the visual calculation of edge-effect depth from the plots of raw data of each individual transect (Chapter 3). The range of edge-effect depths provided by the assessment of each transects raw data was then used to calculate a mean edge-effect depth and its 95% confidence limit for each abiotic factor in each tree species. This mean and the 95% confidence limit provided the full range of potential edge-effect depths for the habitat patches. Significant results from the plots of squared euclidean distances of abiotic data were also applied to the core-area model, the point of highest contrast in the plots suggesting the position of the edge-effect.

Assessment of edge-effect depths (d) were made from the plots of raw density data for those invertebrates showing significant response to edge proximity in Chapter 4, these included the Acarina, Araneae, Coleoptera and Collembola. Few of these plots however
showed any significant edge-effects due to the great intra-sample variation in any given transect. Plots of invertebrate richness and diversity were not used again due to the high levels of intra-sample variation and the lack of any clear patterns. Squared and relative euclidean distance results for invertebrate density and diversity were however applied to the core-area model in the same manner as for the abiotic data. Guild analysis showed few edge-effect depths, where they occurred they followed similar edge-effect depth patterns to the normal invertebrate data.

The information required for the calculation of the core-area model over and above that of edge-effect depth \((d)\) includes the total area \((TA)\) of the fragment in hectares and the perimeter length \((P)\) in metres. These pieces of information were obtained from a number of sources:

\[(TA)\] was obtained from the patch data held on the Forestry Commission sub-compartment data base, which gives accurate figures in hectares of the planting size of all plantation compartments,

\[(P)\] was calculated from 1:10000 and 1:20000 maps of forest patches obtained from the respective Forestry Commission regional offices covering the sample areas.

Total patch area \((TA)\) and perimeter length \((P)\) were used to calculate the Shape Index \((Patton 1975)\) of the research patches using equation 4.1 the results of which are in Table 4.1.
Table 4.1. Forest patch details for research patches in *Picea sitchensis* and *Pinus sylvestris*, required to calculate Shape Index (Patton 1975). Total area (TA) and patch perimeter (P) data obtained from Forestry Commission data base and maps.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th><em>P. sitchensis</em></th>
<th><em>P. sitchensis</em></th>
<th><em>P. sylvestris</em></th>
<th><em>P. sylvestris</em></th>
<th><em>P. sylvestris</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Compartment Code</td>
<td>2544</td>
<td>9556</td>
<td>3607</td>
<td>3616</td>
<td>2103</td>
</tr>
<tr>
<td>Transect Codes</td>
<td>K1, K3, K4</td>
<td>K2</td>
<td>NY1</td>
<td>NY2</td>
<td>NY3</td>
</tr>
<tr>
<td>Total Area Hectares (TA)</td>
<td>63</td>
<td>54.5</td>
<td>7.1</td>
<td>9.2</td>
<td>12.5</td>
</tr>
<tr>
<td>Patch Perimeter (m)</td>
<td>3260</td>
<td>3040</td>
<td>1100</td>
<td>1380</td>
<td>1540</td>
</tr>
<tr>
<td>Shape Index (SI)</td>
<td>1.16</td>
<td>1.16</td>
<td>1.17</td>
<td>1.28</td>
<td>1.23</td>
</tr>
</tbody>
</table>
Once shape index had been calculated, the Laurance and Yensen (1991) core-area model was applied to the data. Calculation of affected area (AA) was by equation 4.2; this was then recalculated (AA\textsubscript{adj}) using equation 4.3. All the research patches in this study had shape indices below 1.5 (Table 4.1) meaning that AA alone would underestimate the quantity of core area. Calculation of AA\textsubscript{adj} compensated for this tendency. The AA\textsubscript{adj} was then subtracted from the total patch area (TA) as in equation 4.4 resulting in a figure for the adjusted core area. From this the proportion of AA\textsubscript{adj} and CA\textsubscript{adj} was apparent and the percentage of the habitat that was CA\textsubscript{adj} could be calculated to investigate the quantity of forest patch under edge and core conditions. The calculation of the percentage allowed comparison with Laurance’s (1991) suggestion of a 50% minimum core area in any habitat patch to maintain viable populations.

4.2.2. Management Patches.

The effects of edge management practices on the proportions of edge and core habitat in plantation patches were explored by applying proposed edge management processes to the research patches, calculating the resulting changes in total area (TA), perimeter length (P) and shape index (SI) and applying a number of mean edge-effect depths to the new patch shapes using the core-area model (Laurance and Yensen 1991). Many methods of edge management for the encouragement of invertebrates, specifically Lepidoptera have been proposed by the Institute of Terrestrial Ecology and the Forestry Commission (Ferris-Kaan 1991), these predominantly rely on the sculpturing and increasing of edge habitat, encouraging plant diversity and open habitat at plantation edges. However the
effects of this increase in edge habitat have not been assessed on the whole invertebrate community and more specifically that of the core habitat. Various forms of edge management including box junctions and bays were applied to the five research patches and the changes in total patch area (TA) and perimeter length (P) calculated, once again allowing the calculation of the Shape Index for the newly shaped patches.

Box junctions are the creation of permanent glades by the removal of plantation corners at the intersections of forest tracks (Greatorex-Davies 1991). Therefore at each corner a square plantation will lose patch area and perimeter length (Figure 4.1a), various depths of box junctions can be used but a number of metres in from each corner are preferred, here distances of 10 and 20 metres were used to establish the effects of different box junction depths, depths proposed by Greatorex-Davies (1991). In general box junctions lead to a reduction in the shape index for the research patches, Table 4.2 showing the effects of box junctions on the patches total area (TA), perimeter length (P) and shape index (SI). A further suggested method for plantation edge management is the removal of areas of trees in bays along the length of plantation edges (Figure 4.1b and c). Again a number of bay sizes and densities have been proposed although a mean size is approximately 30 x 10 metres to encourage light exposure at plantation edges therefore encouraging butterflies (Carter 1991, Greatorex-Davies 1991). Two densities of 30 x 10 metre bays were applied to all the research patches, code Bay 1 represents bays at high densities cut at 30 metre intervals along all the edges of plantations (Figure 4.1b), whilst code Bay 2 represents lower densities of bays, cut at 60 metre intervals along plantation edges (Figure 4.1c). These bays have a considerable effect on the patch resulting in a
Table 4.2. Effects of hypothetical edge management on patch statistics required to calculate Shape Index (Patton 1975), for research patches in *Picea sitchensis* and *Pinus sylvestris*. Total area and patch perimeter data originally obtained from Forestry Commission database and maps, management effects calculated from map manipulation.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th><em>P. sitchensis</em></th>
<th><em>P. sitchensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Compartment Code</td>
<td>2544</td>
<td>9556</td>
</tr>
<tr>
<td>Management Code</td>
<td>Box 10</td>
<td>Box 20</td>
</tr>
<tr>
<td>Management Number</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Total Area Hectares (TA)</td>
<td>62.9</td>
<td>62.7</td>
</tr>
<tr>
<td>Patch Perimeter (m)</td>
<td>3224.9</td>
<td>3189.8</td>
</tr>
<tr>
<td>Shape Index (SI)</td>
<td>1.15</td>
<td>1.14</td>
</tr>
</tbody>
</table>
Table 4.2. continued.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>P. sylvestris</th>
<th>P. sylvestris</th>
<th>P. sylvestris</th>
</tr>
</thead>
<tbody>
<tr>
<td>Compartment Code</td>
<td>3607</td>
<td>3616</td>
<td>2103</td>
</tr>
<tr>
<td>Management Code</td>
<td>Box 10</td>
<td>Box 20</td>
<td>Bay 1</td>
</tr>
<tr>
<td>Management Number</td>
<td>4</td>
<td>4</td>
<td>16</td>
</tr>
<tr>
<td>Total Area Hectares (TA)</td>
<td>7.06</td>
<td>6.9</td>
<td>6.6</td>
</tr>
<tr>
<td>Patch Perimeter (m)</td>
<td>1070</td>
<td>1035</td>
<td>1397.5</td>
</tr>
<tr>
<td>Shape Index (SI)</td>
<td>1.14</td>
<td>1.11</td>
<td>1.53</td>
</tr>
</tbody>
</table>

Management Codes: **Box 10** = 10 metre deep box junctions. **Box 20** = 20 metre deep box junctions. **Bay 1** = 10 x 30 metre deep bays every 30 metres along all plantation edges. **Bay 2** = 10 x 30 metre deep bays every 60 metres along all plantation edges.

Management Numbers: number of corners managed (Box 10/20) or total number of bays cut into perimeter (Bay 1/2) of plantation patches.
decrease in patch area (TA) and increase in perimeter length (P), resulting in considerably higher shape indices (Table 4.2).

Three mean edge-effect depths, 5, 30 and 80 metres, representative of the most extreme and the mean edge-effect depths, were calculated from the previous research data and applied to each of the new patch. These data allowed calculation of the potential reduction in core area due to these specific management practices, which although beneficial to Lepidoptera (Greatorex-Davies 1991) could seriously affect the habitat quantity of core habitat for some invertebrate species.
4.3 Results.

4.3.1 Research Patches.

4.3.1.1 Humidity Core Areas.

A 30 metre relative humidity edge-effect applied to the core-area model for *Picea sitchensis* resulted in edge habitat, with low humidity readings, comprising 15 to 16 percent of the total patch area, resulting in the greatest proportion of the patches (84-85%) having core humidity values (Table 4.3). The smaller patch, 9556 (Table 4.1), due to its reduced area, had a slightly greater proportion of edge habitat, this is due to the size difference alone as it shares an identical shape index with the larger *P. sitchensis* patch (2544).

*Picea sitchensis* patch 2544 from which transects 1, 3 and 4 were sampled, showed a range of edge-effect depths for the three transects from 20 to 60 metres (Table 4.3). Depending on edge-effect depth, the percentage of edge habitat ranged between 10 and 30 % in patch 2544, resulting in 70 to 90% of the patch having relatively stable high humidity core habitat readings. Transect 2 taken in patch 9556 had a visual edge-effect depth of 50 metres, here 26% and 74% of habitat were under edge and core conditions respectively (Table 4.3). It appeared that for relative humidity the two *P. sitchensis* patches were showing similar responses to edge proximity, resulting in similar percentages of edge and core habitats.
Rather than the use of a range of edge-effect depths on the different habitat patches it was preferable to apply a mean with 95% confidence limits to the model. The visual edge-effect depths between 20 and 60 metres gave a mean edge-effect depth of 40 metres for relative humidity in *P. sitchensis*, with an upper 95% confidence limit of 69.1 metres and a lower 95% confidence limit of 11 metres (Table 4.3). When applied to the two *P. sitchensis* patches approximately 20% (11-12 hectares) of the habitat was affected by low humidity levels with 80% (40-50 hectares) having high humidity levels. The higher 95% confidence limit resulted in a significant reduction in the quantity of core area with just 67% for patch 2544 and 64% for patch 2556 remaining under core conditions. This was equivalent to a cut of 20% core area, a drop of approximately 8 hectares with a 19 metre increase in edge-effect depth. The lower 95% confidence limit (11m) resulted in a high percentage of both research patches being under core conditions, nearly 95% in both cases (Table 4.3) with just 5%, or 3.5 hectares of edge habitat.

The *P. sitchensis* patches, with relatively low shape indices and high area supported a 65 to 95% range of core area habitat with high relative humidity levels. This was a considerable range in the percentage area of the habitat, but did not fall below or get significantly near the minimum core area figure of 50% proposed by Laurance (1991). It appeared that the *P. sitchensis* research patches were of a suitable shape and size to encourage large areas of core habitat with high stable humidity readings.
Table 4.3. Proportion of edge and core habitat (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for relative humidity (%) edge-effect depths in *Picea sitchensis* and *Pinus sylvestris* research patches.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Patch</th>
<th>Transect</th>
<th>Edge-Effect Data Type*</th>
<th>Edge-Effect Depth (m)</th>
<th>Total Patch Area (ha)</th>
<th>Edge Area (ha)</th>
<th>Core Area (ha)</th>
<th>% Total Patch Area (Edge)</th>
<th>% Total Patch Area (Core)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea sitchensis</em></td>
<td>2544</td>
<td>1,3,4</td>
<td>combined</td>
<td>30</td>
<td>63</td>
<td>9.5</td>
<td>53.6</td>
<td>15.0</td>
<td>85</td>
</tr>
<tr>
<td></td>
<td>9556</td>
<td>2</td>
<td>combined</td>
<td>30</td>
<td>54.5</td>
<td>8.8</td>
<td>45.7</td>
<td>16.2</td>
<td>83.8</td>
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<td>visual</td>
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<td>63</td>
<td>9.5</td>
<td>53.5</td>
<td>15.0</td>
<td>85</td>
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<td>9556</td>
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<td>visual</td>
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<td>54.5</td>
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<td>26.3</td>
<td>73.7</td>
</tr>
<tr>
<td></td>
<td>2544</td>
<td>3</td>
<td>visual</td>
<td>20</td>
<td>63</td>
<td>6.4</td>
<td>56.6</td>
<td>10.1</td>
<td>89.9</td>
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<tr>
<td></td>
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<td>60</td>
<td>63</td>
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<td>44.8</td>
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<td>71</td>
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<td></td>
<td>2544</td>
<td>1,3,4</td>
<td>95% upper</td>
<td>69.1</td>
<td>63</td>
<td>20.8</td>
<td>42.3</td>
<td>32.9</td>
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<td>2544</td>
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<td>3.5</td>
<td>59.5</td>
<td>5.6</td>
<td>94.4</td>
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<td>2544</td>
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<td>mean</td>
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<td>11.6</td>
<td>42.9</td>
<td>21.3</td>
<td>78.7</td>
</tr>
<tr>
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<td>2544</td>
<td>2</td>
<td>95% upper</td>
<td>69.1</td>
<td>54.5</td>
<td>19.4</td>
<td>35.1</td>
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<td>95% lower</td>
<td>11</td>
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<td>3.3</td>
<td>51.2</td>
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<td>93.9</td>
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<tr>
<td><em>Pinus sylvestris</em></td>
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<td>combined</td>
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<td>3.8</td>
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<td>40.9</td>
<td>59.1</td>
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<td></td>
<td>2103</td>
<td>3</td>
<td>combined</td>
<td>30</td>
<td>12.5</td>
<td>4.3</td>
<td>8.2</td>
<td>34.1</td>
<td>65.9</td>
</tr>
</tbody>
</table>

* edge-effect depth calculated from: **combined** transect data for the respective tree species; **visual** assessment of edge-effect depth from plots of relative humidity data for individual transects; **mean and 95% confidence limits** calculated from range of edge-effect depths provided by visual assessment data.
Table 4.4. Proportion of edge and core habitats (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for temperature (°C) edge-effect depths in *Picea sitchensis* and *Pinus sylvestris* research patches.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Patch</th>
<th>Transect</th>
<th>Edge-Effect Data Type*</th>
<th>Edge-Effect Depth (m)</th>
<th>Total Patch Area (ha)</th>
<th>Edge Area (ha)</th>
<th>Core Area (ha)</th>
<th>% Total Patch Area (Edge)</th>
<th>% Total Patch Area (Core)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea sitchensis</em></td>
<td>2544</td>
<td>1,3,4</td>
<td>combined</td>
<td>20</td>
<td>63</td>
<td>6.4</td>
<td>56.6</td>
<td>10.1</td>
<td>89.9</td>
</tr>
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<td></td>
<td>9556</td>
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<td>combined</td>
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<td>54.5</td>
<td>5.9</td>
<td>48.6</td>
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<td>2544</td>
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<td>visual</td>
<td>30</td>
<td>63</td>
<td>9.4</td>
<td>53.6</td>
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<td>visual</td>
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<td>54.5</td>
<td>5.9</td>
<td>48.6</td>
<td>11</td>
<td>89</td>
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<td></td>
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<td>10</td>
<td>63</td>
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<td>59.9</td>
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<td>2544</td>
<td>4</td>
<td>visual</td>
<td>45</td>
<td>63</td>
<td>13.9</td>
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<tr>
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<td>95% lower</td>
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<td>1.3</td>
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</tr>
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<td>95% upper</td>
<td>64.6</td>
<td>12.5</td>
<td>8.4</td>
<td>4.1</td>
<td>66.8</td>
<td>33.2</td>
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<tr>
<td></td>
<td>2103</td>
<td>3</td>
<td>95% lower</td>
<td>-11.3</td>
<td>12.5</td>
<td>none</td>
<td>&gt;12.5</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* edge-effect depth calculated from: **combined** transect data for the respective tree species; **visual** assessment of edge-effect depth from plots of temperature data for individual transect; **mean and 95%** confidence limits calculated from range of edge-effect depths provided by visual assessment data.
Relative humidity edge-effect depths in *Pinus sylvestris* transects were more variable than those of *P. sitchensis*, with one transect showing an opposite to expected trend of high humidity readings near the edge. This high variation prevented a meaningful mean and 95% confidence limits being calculated. However, from visual inspection of relative humidity plots it appeared that readings stabilised beyond 30 metres, an edge-effect depth similar to that found in *P. sitchensis*. When applied to all three transects core habitat area ranged from 57 to 66% of the habitat. This was a lower proportion of core habitat than that found in *P. sitchensis*, due to the smaller size and higher shape indices of *P. sylvestris* forest patches. Although not dropping below the 50% minimum core habitat level, these values were considerably closer than the *P. sitchensis* results. Potentially, a small variation in this 30 metre figure would drop core area below 50%. The *P. sylvestris* research plantation patches appeared to be planted near the minimum area able to support core humidity habitat.

4.3.1.2 Temperature Core Areas.

Combined, visual and mean edge-effect depths were calculated for temperature data in both tree species (Table 4.4). *Picea sitchensis* showed consistent results with high percentage core areas, none dropping below 70% of total patch area. The combined edge-effect depth of 20 metres applied to both patches gave 89% core area and 11% edge habitat. Visual discrimination of edge-effect depths from the plots of relative temperature gave a range of depths between 10 and 45 metres, resulting in a mean of 26.3 metres and an upper and lower 95% confidence limit of 50 and 2.5 metres respectively. The mean
edge-effect depth gave approximately 86% of habitat as core with lower temperature readings. When applying the 50 metre edge-effect depth, core habitat was reduced to 74%, with the lower 95% confidence limit providing almost 99% core area. In the same way as the humidity data, variation in edge-effect depth was having an effect on core area size in the large and regular shaped *P. sitchensis* patches but failed to reduce core area below 50% of total patch area. For patches of that size and shape, core area with low temperature comprised between 74 and 99% of the patch area similar to the 65 to 95% core area apparent from the relative humidity data. At worst the two *P. sitchensis* research patches were providing a minimum of 65% core habitat defined by high relative humidity and low temperature readings.

The combined temperature edge-effect depths for *P. sylvestris* patches was 30 metres, identical to that of relative humidity, resulting in a percentage core area of habitat figures ranging between 57 to 66% (Table 4.4) depending on habitat patch. Visual depths of edge-effect were however more variable, between 10 and 40 metres, with core habitat areas of 47 to 85%. This provided the first drop of core area below the suggested 50% minimum core area made by Laurance (1991), the patches failing to provide significant quantities of core habitat areas with low temperature levels. This reduction below 50% core area was more extreme when the mean and 95% confidence limits were applied to the three habitat patches.

The mean edge-effect depth for *P. sylvestris* temperature data was 26.7 metres with 95% confidence limits of 64.6 metres and −11.3 metres (Table 4.4). The core-area model could
not be applied to this lower negative edge-effect value, as the result would have been a core area size larger than the original total patch size; the whole patch being considered core habitat. For the mean depth of 26.7m core percentage area ranged between 61 and 69%, however these levels fell considerably when the upper 95% confidence limit was applied. Percentage core area declined to 20 to 33% of research patch area with the edge-effect depth of 64.6m, significantly reducing the core area of these patches. *P. sylvestris* patches were maintaining over 50% patch area levels of core area for relative humidity but, at its most extreme, core temperature conditions could have fallen to just 20% of the patch area, an area of 1.4 hectares (Table 4.4). This would have significantly limited the habitat available to any species dependent on low temperature levels, such as the Collembola.

4.3.1.3 Abiotic Squared Euclidean Distance Core Areas.

Squared euclidean distance (SED) analysis for combined relative humidity and temperature data resulted in a few significant results. The majority of plots showed a peak in SED readings at 2.5m suggesting high contrast between readings taken at 0 and 5 metres, resulting in an edge-effect depth of 5 metres. Incorporation of this 5 metre edge-effect into the core-area model resulted in greater than 90% of total area being core habitat for all patches in both tree species (Table 4.5).
Table 4.5. Proportion of edge and core habitat (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for abiotic squared euclidean distance (SED) edge-effect depths in *Picea sitchensis* and *Pinus sylvestris* research patches.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Patch</th>
<th>Transect</th>
<th>Edge-Effect Data Type*</th>
<th>Edge-Effect Depth (m)</th>
<th>Total Patch Area (ha)</th>
<th>Edge Area (ha)</th>
<th>Core Area (ha)</th>
<th>% Total Patch Area (Edge)</th>
<th>% Total Patch Area (Core)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea sitchensis</em></td>
<td>2544</td>
<td>1,3,4</td>
<td>combined</td>
<td>5</td>
<td>63</td>
<td>1.6</td>
<td>61.4</td>
<td>2.6</td>
<td>97.4</td>
</tr>
<tr>
<td></td>
<td>9556</td>
<td>2</td>
<td>combined</td>
<td>5</td>
<td>54.5</td>
<td>1.5</td>
<td>53</td>
<td>2.8</td>
<td>97.2</td>
</tr>
<tr>
<td><em>Pinus sylvestris</em></td>
<td>3607</td>
<td>1</td>
<td>visual</td>
<td>5</td>
<td>7.1</td>
<td>0.6</td>
<td>6.5</td>
<td>7.8</td>
<td>92.3</td>
</tr>
<tr>
<td></td>
<td>3616</td>
<td>2</td>
<td>visual</td>
<td>5</td>
<td>9.2</td>
<td>0.8</td>
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<td>7.3</td>
<td>92.7</td>
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<tr>
<td></td>
<td>2103</td>
<td>3</td>
<td>visual</td>
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<td>12.5</td>
<td>0.8</td>
<td>11.7</td>
<td>6</td>
<td>94</td>
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</tbody>
</table>

*edge-effect depth defined by peak in SED values calculated from: **combined** transect data for the respective tree species; **visual** assessment of edge-effect depth from individual transect plots.
These results suggest a much greater core area predicted by the use of squared euclidean distance than may actually be the case, when visual assessment of the depth of abiotic edge-effects is considered. Although SED is highlighting the most dramatic point of contrast which results in a 92 to 97% abiotic core area, more subtle effects in temperature and relative humidity, capable of affecting invertebrate communities, may result in core areas closer to 30 to 80% of total patch area. SEDs may therefore be useful in highlighting the maximum point of contrast in transect data but may be of little use in the incorporation into core-area models.

4.3.1.4 Invertebrate Core Areas.

A few plots of the mean invertebrate density concurred in their pattern with the results of the edge core t-test analyses in Chapter 3. In *Picea sitchensis* Coleoptera density was significantly higher in a number of the edge samples, for transect 1 and the combined data this increased density seems to have been concentrated over the first 15 metres. This 15m edge-effect resulted in a 92.4% core area with low coleopteran densities in patch 2544, with just 7.6% edge area with high coleopteran density, and 91.8% core and 8.2% edge habitat in *P. sitchensis* patch 9556 (Table 4.6). All other plots of mean invertebrate density with distance showed no clear patterns with considerable peaks and troughs throughout their length preventing definition of edge-effects.

Three invertebrate orders in *Pinus sylvestris* had density plots whose patterns associated with the significant results of the edge core t-tests. The Acarina, Araneae and
Table 4.6. Proportion of edge and core habitats (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for invertebrate density (m²) edge-effect depths in *Picea sitchensis* and *Pinus sylvestris* research patches.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Taxon</th>
<th>Patch</th>
<th>Transect</th>
<th>Edge-Effect Data Type*</th>
<th>Edge-Effect Depth (m)</th>
<th>Total Patch Area (ha)</th>
<th>Edge Area (ha)</th>
<th>Core Area (ha)</th>
<th>% Total Patch Area (Edge)</th>
<th>% Total Patch Area (Core)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea sitchensis</em></td>
<td>Coleoptera</td>
<td>2544</td>
<td>1,3,4</td>
<td>combined</td>
<td>15</td>
<td>63</td>
<td>4.8</td>
<td>58.2</td>
<td>7.6</td>
<td>92.4</td>
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<td>4.5</td>
<td>50</td>
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<td>Araneae</td>
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<td>visual</td>
<td>10</td>
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<td>7.9</td>
<td>14.4</td>
<td>85.6</td>
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<td>0.5</td>
<td>93.5</td>
<td>6.5</td>
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<td>combined</td>
<td>80</td>
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<td>8.5</td>
<td>0.7</td>
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<td>7.5</td>
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<tr>
<td></td>
<td>Collembola</td>
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<td>9.9</td>
<td>2.6</td>
<td>79.3</td>
<td>20.7</td>
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*edge-effect depth calculated from: combined transect data for the respective tree species; visual assessment of edge-effect depth from plots of invertebrate density data for individual transect.*
Collembola all showed density plots with definable edge-effect depths. For transect 1 Acarina were higher but variable beyond a depth of 30 metres. A 30 metre edge-effect depth applied to patch one in *Pinus sylvestris* resulted in 42.7% edge habitat and 57.3% core (Table 4.6). The plot of Araneae for transect 2 highlighted an edge-effect depth of 10 metres with higher but variable densities beyond this point, so 14.4% of the habitat had low densities of spiders associated with edge conditions, whilst 85.6% of the patch (7.9 hectares) supported high core densities of Araneae (Table 4.6). Collembola showed an edge-effect depth of 80 metres in *Pinus sylvestris* for transect 3 and the combined data, while collembolan density increased considerably beyond this depth, supported by the result of the t-tests (Chapter 3). When applied to all three *Pinus sylvestris* patches, edge habitat with low collembolan densities occupied 79.3 to 93.5 % of the forest patches (Table 4.6), with just 6.5 to 20.7 % core habitat to support high collembolan densities.

4.3.1.5 Invertebrate SEDs and REDs Core Areas.

Acarina density, diversity and total invertebrate diversity showed definable edge-effect depths from the data reported in Chapter 3. For *P. sitchensis* transect 1 Acarina density and diversity showed a 5 metre edge-effect depth resulting in 2.6% edge and 97.4% core habitat (Table 4.7), with higher densities being recorded in the core habitat and higher diversity in the edge habitat. In the same *P. sitchensis* patch an Acarina diversity edge-effect was recorded at 25m (transect 4) increasing the edge habitat percentage to 12.5% (Table 4.7). These *P. sitchensis* patches have apparently large core areas suitable for high levels of Acarina densities but may be limited in the quantity of edge habitat they are
providing, which in turn will limit potential species diversity. The only other edge-effect depth for *P. sitchensis* was a 30m edge-effect in total invertebrate diversity for *P. sitchensis* transect 1; again showing higher total diversity in the edge. Almost fifteen percent of the habitat was available to support this increased level of diversity at the edge, with 85% of the patch supporting lower total species diversity (Table 4.7).

Total invertebrate diversity showed a 75m edge-effect depth in the combined *P. sylvestris* data, this edge-effect reduced core habitat to between 11 and 24.9% of patch area (Table 4.7). The result was a significant reduction in the area suitable to support high invertebrate diversity, as core habitat showed significantly higher diversity than edge habitats. The only invertebrates to show an edge-effect in their density data for *P. sylvestris* were the Coleoptera. In transect 2 significantly higher densities of beetles were recorded in the edge habitat with an SED depth of 5 metres, resulting in just 7.3% of the habitat area supporting high densities (Table 4.7). In contrast to this, transect 3 showed an increased edge-effect depth of 30 metres with higher densities reported in the core habitat for Coleoptera, 66% of the patch being available to support these high densities.

### 4.3.2 Management Patches.

Three mean edge-effect depths (5, 30 and 80 metres) representing the least and most extreme edge-effects recorded from the research data above, were applied to the five patches each under the four new management schemes (Box 10, Box 20, Bay 1 and Bay 2). In general the application of Box junctions (Box 10 and 20m) to the habitat patches
Table 4.7. Proportion of edge and core habitats (hectares) and percentages for invertebrate squared and relative euclidean distances (S/RED), for density and diversity, in *Picea sitchensis* and *Pinus sylvestris* research patches.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Taxon</th>
<th>Patch</th>
<th>Transect</th>
<th>Edge-Effect Data Type*</th>
<th>Edge-Effect Depth (m)</th>
<th>Total Patch Area (ha)</th>
<th>Edge Area (ha)</th>
<th>Core Area (ha)</th>
<th>% Total Patch Area (Edge)</th>
<th>% Total Patch Area (Core)</th>
</tr>
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<td>visual</td>
<td>5</td>
<td>63</td>
<td>1.6</td>
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<td>61.4</td>
<td>2.6</td>
<td>97.4</td>
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<td>55.1</td>
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<td>85</td>
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<td>visual</td>
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<td>9.2</td>
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<td>7.3</td>
<td>92.7</td>
</tr>
<tr>
<td></td>
<td>Total diversity</td>
<td>2103</td>
<td>3</td>
<td>visual</td>
<td>30</td>
<td>12.5</td>
<td>4.3</td>
<td>8.2</td>
<td>34</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td>Total diversity</td>
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<td>1</td>
<td>combined</td>
<td>75</td>
<td>7.1</td>
<td>6.3</td>
<td>0.8</td>
<td>88.9</td>
<td>11.1</td>
</tr>
<tr>
<td></td>
<td>Total diversity</td>
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<td>75</td>
<td>9.2</td>
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<td>89</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Total diversity</td>
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<td>combined</td>
<td>75</td>
<td>12.5</td>
<td>9.4</td>
<td>3.1</td>
<td>75.1</td>
<td>24.9</td>
</tr>
</tbody>
</table>

* edge-effect depth defined by peak in SED/RED values calculated from: **combined** transect data for the respective tree species; **visual** assessment of edge-effect depth from individual transect plots.
resulted in a reduction in both patch area and perimeter length leading to a lower shape index value (Table 4.2). The application of various densities of bays into the patches resulted in a slight decrease in total area but a sizeable increase in perimeter length resulting in considerably higher shape index values (Table 4.2).

4.3.2.1 *Picea sitchensis*.

The *P. sitchensis* patches 2544 and 9556 are relatively large square patches whose corners were smoothed by the application of Box junction management, resulting in lower shape index values closer to 1, denoting a more circular patch (Table 4.8). This drop in the shape index values was a result in a reduction in the total area and the perimeter length of the patch.

The application of Box junctions to the *P. sitchensis* patches results in very little variation in the percentages of edge and core habitat when the three edge-effect depths (5, 30 and 80m) are calculated with the core-area model (Table 4.8). The results for both Box 10 and Box 20 do not vary from those percentages reported when the three depths are applied to the original research patches (Table 4.8), with approximately 97% core habitat for the 5 metre edge-effect, 85% for the 30 metre and 61 % for the 80 metre edge-effect depth. Therefore application of Box junctions to large *P. sitchensis* patches appears not to alter the shape and area of these patches enough to result in significant increases in edge habitat or a reduction of core habitat.
Table 4.8. Proportion of edge and core habitats (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for mean edge-effect depths (5, 30 and 80 m) in *Picea sitchensis* plantations under various hypothetical edge management strategies.

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Management Codes: None = original patch size and shape.  
Box 10 = 10 metre deep box junctions.  
Box 20 = 20 metre deep box junctions.  
Bay 1 = 10 x 30 metre deep bays every 30 metres along all plantation edges.  
Bay 2 = 10 x 30 metre deep bays every 60 metres along all plantation edges.
The alterations in percentage of edge and core habitat in the two *P. sitchensis* patches are more significant with the cutting of bays into the patches (Table 4.8). The high densities of Bays, cut every 30 metres along the perimeters, result in a significant increase in the proportion of edge habitat in patch 2544 compared to the original patch figures, being 1% higher for the 5 metre edge-effect, 5% for the 30 metre and 13% for the 80 metre edge-effect (Table 4.8). These increases in edge habitat result in a reduction of core habitat, which for the 80 metre edge-effect depth drops below the 50% core habitat level, recommended by Laurance and Yensen (1991). The application of a lower density of Bays to this patch (2544) also leads to higher percentages of edge habitat and a corresponding reduction in percentage core habitat although this does not drop below the 50% level (Table 4.8). The increased shape index values created by the convoluted perimeter and loss of habitat area have lead to a significantly higher quantity of edge habitat in this patch which at the most extreme edge-effect depth (80m) leads to over half of the patch being affected by edge proximity. This pattern is seen to a more extreme degree in the slightly smaller *P. sitchensis* patch (9556).

The smaller *P. sitchensis* patches (9556) percentage edge habitat is increased for all edge-effect depths when the patch has undergone dense bay cutting (Bay 1). The 80 metre edge-effect depth results in 18% more of the patch being edge habitat than for the original patch (Table 4.8), giving a total of 56.3% edge habitat resulting in less than 50% core habitat. This reduction below the 50% core habitat level is also recorded when the bays are at low density (Bay 2) which results in 51.3% of the patch being edge habitat. It therefore appears that even for relatively large habitat patches, such as those found in *P.*
sitchensis, the cutting of bays into the edge of the patches leads to such an alteration in the size and convolution of the edge and alteration of the shape index that edge habitat is significantly increased, sometimes to the detriment of core area.

4.3.2.2. Pinus sylvestris.

All three *P. sylvestris* plantation patches were considerably smaller than the *P. sitchensis* patches and suffer from more extreme core area loss than in the previous analysis under the management strategies tested. The changes in the percentage of edge and core habitat after the application of different depths of Box junctions can be seen in Table 4.9. For both depths (10 and 20m) the percentage of the habitat affected by the presence of edge is lower than for the original patch (Table 4.9). Therefore for an edge-effect depth of 5 metres all patches have over 90% core area reducing to approximately 60% when the edge-effect depth is increased to 30 metres. However the extreme edge-effect depth of 80 metres results in very low percentages of core habitat as it did in the original patches, although the quantities of core habitat are all slightly higher for the Box patches (Table 4.9). For the 80 metre edge-effect depth core areas range between 9 and 21% equivalent to just 0.8 to 2.7 hectares, these percentages are considerably below a quantity deemed adequate to support core communities (Laurance and Yensen 1991) which could be being excluded from these patches.

When the Bays are applied to the three *P. sylvestris* patches considerable increase in the percentage of edge habitat is seen (Table 4.9), resulting in loss of core habitat. In general
Table 4.9. Proportion of edge and core habitats (hectares) and percentage of total patch area calculated using the core-area model (Laurance and Yensen 1991), for mean edge-effect depths (5, 30 and 80 m) in *Pinus sylvestris* plantations under various hypothetical edge management strategies.

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Management Codes: None = original patch size and shape.  
Box 10 = 10 metre deep box junctions.  
Box 20 = 20 metre deep box junctions.  
Bay 1 = 10 x 30 metre deep bays every 30 metres along all plantation edges.  
Bay 2 = 10 x 30 metre deep bays every 60 metres along all plantation edges.
the most extreme increases in percentage edge area are from the high bay density (Bay 1), particularly when the 80 metre edge-effect is applied. This combination of highly convoluted perimeters and loss of total area, combined with a large edge-effect results in all the patches being edge habitat, with no core conditions present (Table 4.9). However the 30 metre edge-effect depth also results in a drop below 50% core habitat in patches 3607 and 3616 (Table 4.9), the two smaller *P. sylvestris* patches. Only the 5 metre edge-effect depth shows limited effect on the quantity of core habitat with approximately 90% core habitat maintained in all patches under both management techniques. Therefore the cutting of a number of bays into the edge of relatively small plantation patches can result in extreme effects on the quantity of core habitat and therefore the species adapted to the habitat type.
4.4 Discussion.

The research patches in both tree species have low shape indices, figures nearing 1, defining a regular shape such as circles or squares (Patton 1975), and relatively high patch area for conifer species planted in UK plantations. These patch features were deliberately selected to ensure that even with extensive edge-effects core habitat would be likely to be encountered, allowing the analysis of differences between edge and core communities in the previous chapter. The presence of both edge and core habitat was confirmed by the results in Chapter 3, where a number of significant differences between the habitats were reported in both abiotic conditions and invertebrate communities. Analysis of the depth of the edge-effects in the various factors investigated was achieved using raw data plots or squared and relative euclidean distances with depths ranging between 5 and 80 metres. As edge-effect depths had been defined and core areas were present the Laurance and Yensen (1991) core-area model was used to define the area in hectares and the percentage of each patch under the two habitat types. The model highlighted the quantity of the patch under the different abiotic conditions, either high temperature and low humidity of the edge habitat or high humidity and low temperature of the core. Further application of the model to significant invertebrate results was performed assessing the quantities of the different habitats preferred by key taxa.

In addition to the quantification of edge and core habitat of the research patches, analysis was performed on the patches after the application of edge management. The desire to create edge habitat is driven by the concept that the habitat supports a diverse invertebrate
community caused by the fusion of the communities of adjoining habitats (Helle and Muona 1985, Baldi and Kisbenedek 1994, Bedford and Usher 1994, Abensperg-Traun et al. 1996). Application of these models have been shown to encourage lepidopteran species and herbaceous plant species in conifer plantation edges (Anderson and Buckley 1991, Carter 1991, Greatorex-Davies 1991, Warren 1991), however the effect on other invertebrate species within the forest system particularly the canopy invertebrates has not been researched. The analysis of management techniques here, aims to highlight the changes these activities have on the quantities of edge and core habitat within conifer plantations and the knock-on effect these may have for invertebrate communities living in the two habitat types.

4.4.1 Picea sitchensis Patches.

Abiotic data showed clearly defined edge-effects ranging between 11 and 69 metres for relative humidity and 2.5 to 50 metres for temperature in Picea sitchensis. Combined abiotic edge depth calculated by the squared euclidean distance method suggested an edge-effect depth of just 5 metres in both tree species. The large total area of the Picea sitchensis research patches resulted in a high percentage of the patches showing core conditions, even under the greatest recorded edge-effect depth. For relative humidity the edge-effect depth of 69.1 metres resulted in 64.5 to 67.1% of the two P. sitchensis forest patches being core area. Well over half of the forest patch, approximately 32-45 hectares therefore had high humidity levels, benefiting small humidity-dependent invertebrates of the core area. Similar proportions of the P. sitchensis patches had low temperature
readings, at worst just 73-75 percent or 40-47 hectares of the forest patches being core area with low temperature. The presence of core area would be lost for these edge-effect depths if the forest patches dropped below approximately 25 hectares.

The *P. sitchensis* patches appear to have clearly different proportions of edge and core habitat defined by abiotic conditions, suggesting an unequal balance of habitat towards the core benefiting invertebrate species biased towards core habitat. The patches are therefore potentially capable of supporting large quantities of invertebrates, which inhabit core conditions. However more invertebrate species respond positively to the edge habitat of *P. sitchensis* than the core, the exception being the Collembola and Acarina, therefore a bias towards core habitat may be limiting the quantity of edge habitat which supports higher invertebrate richness and abundance, limiting overall invertebrate richness in the patches.

Just two taxa showed high densities in the core area of *P. sitchensis* the Collembola and Acarina. Collembolan densities were three times higher in the core almost solely accounted for by *Entomobrya nivalis*. This species is environmentally sensitive, as are all collembolans (Lambert 1970, Hopkin 1997, Hopkin 1998), probably preferring the higher humidity and more stable conditions of the core habitat, however *E. nivalis* is widespread throughout various habitat types in the UK and is not necessarily an important conservation species (Hopkin 1997). However, another species, the less common *Sminthurus fuscus*, showed higher densities in the edge habitat and an increase in the proportion of this area by edge management processes would encourage this species.
Acarina although showing higher densities in the core area of one of the transects showed higher densities in the edge of another, and consistently higher diversities in the edge. Therefore the encouragement of large areas of core habitat within *P. sitchensis* plantation patches would benefit a single common species of Collembola but few other invertebrates, whereas balancing the proportion of the patch towards edge habitat might provide greater benefits for a diverse invertebrate community in the plantation patch.

Over and above *S. fuscus* a number of other invertebrate species responded positively to the edge habitat in *P. sitchensis* (Chapter 3). Seven taxa including various Coleoptera (*Aphidecta obliterata*), Diptera, Hemiptera, Acarina and Araneae (Linyphiidae) showed increased densities in the edge habitat of *P. sitchensis*, a response to increased food supplies, the greening of plantation edges and their structural complexity (Forman and Godron 1986, Lovejoy *et al.* 1986, Williams-Linera 1990, Chen *et al.* 1992). Various guilds also responded positively to these edge areas, herbivores, scavengers and tourists showing higher densities in the edge zone. Within order, guild responses were also reported with both Acarina detritivores/fungivores and predators being more species rich in the edge. Coleoptera showed multiple responses, denser herbivorous and predatory populations in the edge, the herbivores also being more species rich. These invertebrate communities were significantly higher in density and richness at least over the first 10 metres of the *P. sitchensis* patches, leading to approximately 5% of both patches total area supporting higher densities, equivalent to 2.73 to 3.15 hectares of habitat (Table 4.6-4.7).
Therefore the greatest proportion of *P. sitchensis* patches are given over to core habitat, supporting few invertebrate species at low densities, with a relatively narrow but invertebrate abundant and species rich strip of edge habitat bordering the patch. The edge is providing a habitat with plenty of food sources and suitable conditions (although they are warmer and less humid that might be expected) supporting an important invertebrate community. The core habitat of the non native *P. sitchensis* may be too humid and cool for invertebrate communities originally adapted to the slightly warmer and less humid native *P. sylvestris* canopy.

The balance towards edge habitat in the invertebrate community begs the question; ‘are the present size and shape of *P. sitchensis* patches in Kielder forest providing enough edge habitat to support a full and stable invertebrate community?’ It is difficult to calculate minimal viable population (MVP) sizes for particularly small organisms such as invertebrates (Muhlenberg *et al.* 1991), due to the problems of estimating their habitat use. However areas of 2 to 5 hectares and 10 hectares of core oak/hornbean woodland have been proposed for carabid beetles and wandering spiders respectively (Mader 1984). The *P. sitchensis* edge habitat is at times below these proposed suitable areas for some invertebrate species and is distributed in a narrow strip. Therefore management activities resulting in larger areas and a greater proportion of the habitat providing edge conditions would result in a more stable quantity of habitat and therefore diverse invertebrate community in *P. sitchensis* plantations. The patches may therefore benefit from the edge management proposed by Greatorex-Davies (1991) which results in increased edge habitat.
The removal of areas of trees along the perimeter of plantation patches results in reduced patch area and increased perimeter length, changing the patches shape index (Table 4.2), Box junctions leading to a fall in shape index with Bays increasing the value of the index. Table 4.8 shows the results of the application of edge management to the two *P. sitchensis* patches under various edge-effect depths. The 30 metre edge-effect depth, equivalent to the area supporting higher total invertebrate diversity, when applied to the patches with Box junctions leads to a loss of edge habitat, approximately 0.1 to 0.2 of a hectare, compared to the original habitat patch (Table 4.8). A similar loss of edge habitat is seen for the 5 metre edge-effect depth when Box junctions have been applied, a loss of habitat supporting particularly high Acarina diversity.

In contrast the cutting of Bays into the *P. sitchensis* patches resulted in the desired increase in edge habitat. Bays 10 x 30 metres cut every 30 metres along the whole perimeter with a 30 metre edge-effect increased edge habitat by approximately 5% (Table 4.9). This is a gain of 3 hectares in both patches, with an increase of just 0.5 of a hectare for the 5 metre edge-effect depth. Similar sized bays cut at a lower density, every 60 metres along the perimeter increased edge habitat to a lesser degree, just 0.4 hectare increase for 5 metre edge-effect depth and a 2 hectare increase for the 30 metre edge-effect.

With many invertebrates and guilds showing increased densities and diversities in the edge habitat of *P. sitchensis*, maximisation of this habitat type balanced against timber production should be a key initiative if invertebrate conservation is an aim. Kielder Forest
Park in Northumberland is the largest sustained yield forest in Britain dedicated to timber production, conservation and amenity development. The conservation policy centres on three principles: creating diversity, conserving and enhancing natural habitats, and the conservation of rare and protected species (Probert et al. 1996). An important aspect of this conservation aim is the maintenance of insect diversity and abundance and the protection of key species, the conservation of insects not only being a key aim per se but an important maintenance of food supplies for birds. At present much of this is achieved by the management of open habitats and the planting of new areas of deciduous species (Probert et al. 1996). However improved management of the conifer plantations by cutting Bays into the patches or reducing patch size could considerably increase the quantity of edge habitat in the landscape as a whole. This would encourage lepidopteran species as suggested by Greatorex-Davies (1991) but also high abundances and diversities of various invertebrate species associated with the canopies of *P. sitchensis* and the bird communities they support.

**4.4.2 Pinus sylvestris Patches.**

*Pinus sylvestris* plantations in contrast to *P. sitchensis* have a smaller patch size averaging 8.15 hectares and higher shape indices (Table 4.1), these features resulted in small areas of core habitat compared to *P. sitchensis* for both abiotic and invertebrate edge-effects. A low quantity of core habitat would be of little importance if like *P. sitchensis* the invertebrate species in *P. sylvestris* responded predominantly to the edge habitat. However in contrast most positive responses in invertebrate densities and
diversities were seen in the core habitat of *P. sylvestris* which constitutes a smaller proportion of patch area. Therefore unlike *P. sitchensis* where edge habitat needs to be encouraged, core habitat needs to be maximised in *P. sylvestris*.

Temperature and relative humidity in *P. sylvestris*, although more variable than *P. sitchensis* (Chapter 3) showed in general similar patterns with increased temperature and reduced humidity in the edge zone. The visual assessment of the edge-effect depths for temperature and humidity resulted in 26.7 and 30 metre edge-effects respectively, giving between 4.1 and 8.7 hectares core habitat in the plantation patches (Table 4.3 and 4.4). The SED plot for abiotic conditions suggests an even smaller edge-effect depth of just 5 metres, with 6.5 to 11.7 hectares of core habitat. It is likely however that this is underestimating the penetration of abiotic edge-effects suggesting that there is less edge habitat than actually present. Although over 50% of the *P. sylvestris* patches have core abiotic conditions with high humidity and low temperature, placing them above the 50% minimum habitat proposed by Laurance and Yensen (1991), this equates to just 4.1 to 8.7 hectares of forest habitat. These are relatively small areas highly vulnerable to detrimental effects from surrounding habitat or activities rapidly increasing edge habitat. Indeed under the most extreme abiotic edge-effect depth, the 95% upper confidence limit less than 50% of these *P. sylvestris* patches support core abiotic conditions just 1.4 to 4.1 hectares (Table 4.4). These particular *P. sylvestris* plantation patches are supporting small areas of habitat with core abiotic conditions of low temperature and high humidity.
Invertebrates showing a positive response to core habitat in *P. sylvestris* include the Acarina (*Anystis sp.*, *Chamobates sp.* and *Cymbaeremaeus sp.*), Collembola (*Entomobrya nivalis*) and Araneae (*Drapetisca socialis* and *Leptephyantes expunctus*) responding at both the ordinal and species level, with no invertebrates found in higher densities and diversities in the edge of *P. sylvestris*. Acarina show increased densities, species richness and diversity rates beyond 30 metres from plantation edge resulting in at most 4 hectares of the forest patch supporting high densities. This preference for core habitat is shown particularly by three species the predatory *Anystis sp.* (Prostigmata), and the detritivores *Chamobates sp.* and *Cymbaeremaeus sp.* (Oribatida). Although the Collembola and Acarina are small they are considered to be important in canopy communities performing many important habitat functions and providing food sources for larger predatory species (Walter and O’Dowd 1995, Winchester and Ring 1996, Winchester 1997b, Hopkin 1998, Walter and Behan-Pelletier 1999).

Collembola show a rapid increase in densities beyond 80 metres, this increase as in the *P. sitchensis* patches is almost completely accounted for by *Entomobrya nivalis*. When applied to the research patches an 80 metre edge-effect depth left just 0.5 to 2.6 hectares of core habitat supporting high collembolan densities. These are particularly small areas of core habitat open to disturbance by natural events; considerably larger patches are required to support core areas for the Collembola with their 80 metre edge-effect. Indeed research patch area would have to be increased to a minimum of 50 hectares to provide 50% core habitat, some 25 hectares. However somewhat smaller patches than these could provide reasonable areas for the Collembola depending on their MVP requirement. A
similar extreme edge-effect depth is seen for total invertebrate diversity in the SED analysis, some 75 metres again resulting in just small areas of core habitat, 0.8 to 3.1 hectares.

The Araneae, particularly the woodland specialist species *Drapetisca socialis* and *Lepthyphantes expunctus* show increased densities in core areas of *P. sylvestris*. From their density data plots higher densities occur beyond a depth of 10 metres, this leads to a larger quantity of the patches providing suitable habitat (circa. 7.9 hec) than for the Collembola and total invertebrate diversity. *Drapetisca socialis* is a nationally widespread species building its webs on the bark of many tree species however although *L. expunctus* is widespread on pines in southern England in is scarce in more northerly regions (Roberts 1987, Parrack pers. comm.). Its presence here in the relatively northerly area of the North York Moors is therefore unusual and makes it worthy of encouragement in the habitat, again possible by increasing the quantity of patch area beyond 10 metres from plantation edge.

Therefore patch size and shape in these research *P. sylvestris* patches could be acting as a limiting factor on the development of large viable populations of a diverse invertebrate community. This could be especially important due to the native status of *P. sylvestris*, as it is likely to support a more diverse and natively important invertebrate fauna than the imported *Picea sitchensis* (Southwood 1961, Welch 1986, Denno and Roderick 1991), it should be planted in larger areas to encourage the many core-preferring invertebrate species.
For the *P. sylvestris* plantation patches a range of edge-effects were gathered from 5 to 80 metres which resulted in between 8.4 and 0.5 hectares of core habitat within the patches, these areas being the preferred habitat of a wide range of invertebrate species. If the preferred habitat of these species is to be encouraged particularly that beyond 80 metres from the edge where total invertebrate diversity is shown to increase, then *P. sylvestris* plantation patches should not fall much below 7 hectares, and/or shape index should not significantly increase. If size was reduced or shape index increased core habitat could be severely reduced or lost completely resulting in reduction in habitat area suitable to support viable populations of the invertebrate species.

Application of the various forms of edge management to the three small *P. sylvestris* patches resulted in considerable changes in the quantities of core habitat, particularly with the cutting of Bays into the plantation edges. Both densities of Bays resulted in the complete loss of core habitat in all three patches with an edge-effect depth of 80 metres and considerable reductions in core area with the 30 metre edge-effect depth (Table 4.9). The loss of core habitat would result in the loss of the dense and diverse populations of invertebrates found in the canopy of these areas, reducing the overall invertebrate diversity of the plantation. The cutting of Box junctions at the corners of plantations resulted in a less dramatic loss of core habitat, although still reducing the quantity to below adequate levels with a minimum of 0.8 hectares of one patch being core. It appears that the application of edge management to these *P. sylvestris* patches would succeed in increasing the quantity of edge compared to core habitat, however this would result in an overall loss of invertebrate diversity.
Therefore different management processes are required for the two conifer species to encourage canopy invertebrate abundance and diversity. The application of edge management in *P. sylvestris* is inappropriate, management effort should be directed towards the encouragement of core habitat by either increasing patch size or reducing shape index, by making the patches more even shapes (squares/circles). In contrast the large *P. sitchensis* patches benefit from the application of edge management with the increase in edge habitat that it brings. Bays and Box junctions cut into *P. sitchensis* patches would result in an increased quantity of edge habitat in the landscape associated with an increase in invertebrate species abundance and richness.

4.4.3 Application of the Core-Area Model.

From the data analysed here in general the Laurance and Yensen (1991) core-area model is a relatively simply executed and useful tool in the quantification of edge and core habitat in UK conifer plantations. Although a number of issues arise with its application; firstly, the accuracy with which the edge-effect is defined and secondly the usefulness of the suggestion of a 50% minimum core area proportion.

Criticism of the core-area model has highlighted its over simplicity, lacking inclusion of all possible edge-effect sources (Malcolm 1994). Any given point in a habitat patch will be affected by the nearest edge but also, to a lesser degree by those at a greater distance, resulting in a combined edge-effect depth for that point. Malcolm (1994) developed a more additive model which predicted combined edge-effect more accurately than non-
additive methods such as the Laurance and Yensen (1991) model. However the Malcolm
model is more complex to perform, and accentuates the problem of field assessment of
dge-effect depths. It may be that the simplicity of the Laurance and Yensen (1991)
model is its strength, the use of a single edge-effect depth and the easily obtained
perimeter length and patch area data makes it easy for habitat managers to calculate the
proportions of edge and core habitat within their forests, enabling decisions to be made
cerning conservation aims and management processes. A further benefit being the
ease of manipulation to predict the effects of management processes on specific habitat
patches.

Definition of the edge-effect depths is a potential problem with the Laurance and Yensen
(1991) core-area model with the various techniques elucidating very different edge-effect
depths, necessitating careful selection of the method used. The evidence that the *P.
sylvestris* plantation patches have low quantities of core habitat would be unclear if
alysis were solely performed on the definition of edge-effect depth from squared
euclidean distance analysis rather than from visual assessment. For both tree species the
most common extreme point of contrast in the SED plots occurs over the first 5 metres of
the plots, suggesting an edge-effect depth of just 5 metres. When incorporated into the
core-area model this depth overestimates the quantity of core habitat, an issue particularly
important in *P. sylvestris* where the quantity of core area is vital. The use of SED/RED
has been useful in defining large landscape boundary positions (Johnson *et al.* 1992),
however it is of limited use when trying to accurately define edge-effects across small
habitat boundaries for specific species in conifer plantations, always appearing to
underestimate the depth of the edge-effect. Whereas edge-effect depths are more likely to average approximately 15 metres and range between 10 and 80 metres with visual assessment of the abiotic and invertebrate data. These values, particularly when taken from means of data from replicate transects result in more realistic assessment of the quantities of edge and core habitat in the patches. Therefore careful consideration must be given to the method of edge-effect definition and the design of research ensuring adequate replication to construct means and 95% confidence limits from the often highly variable invertebrate data.

As discussed Laurance and Yensen (1991) proposed the figure of 50% core habitat as a useful guide line in the achievement of adequate quantities of core habitat in fragment patches. However this figure can be misleading and closer attention should be paid to the actual quantity in hectares of core area that is being achieved, particularly when the habitat patches are small. In a number of results the *P. sylvestris* patches are reported as supporting considerably over 50% core habitat however in reality this equates to just a few hectares of forest habitat, particularly when edge management has been performed on the patches (Table 4.9). From the percentage value the patches may be considered to contain ample quantities of core habitat however in reality they may not be large enough to support stable minimum viable populations (MVP) (Muhlenberg *et al.* 1991, Schonewald-Cox and Buechner 1991). A second issue with the 50% recommendation is the relative value of the two habitat types, there is little point in achieving over 50% core habitat if the most ecologically important habitat is that at the edge of plantation patches, as it is in the case of *P. sitchensis*. Attention needs to be paid to the species under
consideration, its habitat requirements to support MVP and then concentration on the area in hectares being achieved by the habitat patch in question.

As Laurance and Yensen (1991) showed with hypothetical data and plant field data, the core-area model is a useful tool in fragment analysis at the regional or sub-regional level in habitats with similar edge forms, this appears to be the case with invertebrate field data also. The model here proved to be a strong method in quantifying edge and core habitat and extrapolating these to hypothetical situations such as edge management in two species of conifers under plantation systems in the UK. The model should provide a useful tool in the future for assessing the proportions of important habitat types (either edge or core) in conifer plantation patches to maximise species diversity within these systems. In addition it should enable the detailed assessment of the effects of management processes on the diversity of the habitat before they are implemented, preventing catastrophic loss of species due to inappropriate management activity.
Chapter 5. Tree Species.

5.1 Introduction.

The invertebrate communities occurring on two tree species, *Pinus sylvestris* and *Picea sitchensis* have been examined previously with reference to plantation edge proximity, here variations in invertebrate communities between the two species will be explored. No two plant species, even those from the same genus, will have an identical complement of invertebrates (Southwood *et al.* 1982 a and b, Strong *et al.* 1984, Basset *et al.* 1996), particularly the herbivores associated with that plant, indeed no two trees of the same species will have an identical complement of invertebrates (Hunter 1997). This specific complement of invertebrates develops when the tree is young, for example distinct Heteropteran communities have been shown to establish on young pines, remaining consistent throughout the trees lifetime (Cmoluchowa and Lechowski 1993). Southwood *et al.* (1982b) reported a significant difference in population size and the proportion of invertebrates in each taxon on British deciduous trees, all differences between tree species were greater than within tree species. The predatory guild on different tree species was also found to be more similar than the phytophagous guild on the trees (Southwood *et al.* 1982b), highlighting the specificity of the phytophagous guild to specific plant species and the closer association these invertebrates have to their host tree compared to the predators (Southwood *et al.* 1982b). The differences seen in the communities living on plants result from a number of factors relating to the plant’s historical presence in an area, its abundance, both historically and recently, its chemistry,
structure and the region and habitat in which it grows, these combine to form a unique influence on the invertebrate community altering its structure and complement.

5.1.1 Plant / Invertebrate Abundance.

*Pinus sylvestris* and *Picea sitchensis* show distinct variations in the features mentioned above, leading to expected differences in the invertebrate communities they support, particularly the species present, the species richness, diversity and guild composition. *Pinus sylvestris* is native to the UK naturally found in the Highlands of Scotland, although now widely established in plantations in the south and east of England where it thrives in the quick draining soils and warm temperatures (Mitchell 1985). Branch development in *P. sylvestris* occurs in annual whorls with lower branches dying back, resulting in a relatively high thin canopy which allows large quantities of through radiation (Ford 1985), leading to an abundant and diverse understory even under plantation conditions (Simmons and Buckley 1992).

In contrast *Picea sitchensis* is a non-native species introduced to the UK in 1831 from British Columbia, Canada (Peterken 1996). Its rapid growth of up to 1.3 metres per annum has made it popular as a timber producing plantation tree (Mitchell 1985) indeed *Picea sitchensis* is now the most abundant tree in Britain, with 70% of all woodland being coniferous and the greatest proportion of this being *P. sitchensis* (Peterken 1996). Planting is concentrated in northern regions of England and Scotland, the species thriving on heavy soils and able to cope with high rainfall (Mitchell 1985). The growth form of *P.*
sitchensis is different to that of P. sylvestris with branches occurring at more regular intervals on the trunk and failing to completely die back as canopy closure is achieved. This results in a dense and deep canopy complex with high levels of dead organic matter (Ford 1985), limiting understory development (Simmons and Buckley 1992).

The length of the historical presence of plants in an island flora, such as the two conifer species in the British Isles, has a considerable effect on the invertebrate communities expected on those plant species. It has been proposed that native species, and therefore those that have been in the flora for a considerable time will support a more species-rich invertebrate community (Southwood et al. 1982a, Claridge and Evans 1990), particularly for species closely associated with the plant (herbivores/phytophages). Southwood et al. (1982a) found no significant difference in the species richness and diversity of guilds, other than the phytophages, on introduced compared to native deciduous trees in Britain and South Africa. Simandl (1993) also found high densities of primary consumers in P. sylvestris monocultures, showing that invertebrates more closely associated with the trees, the first-order consumers (phytophages), show higher density and diversity on native species, developing associations with introduced trees slowly.

An early examination of the association of invertebrate species richness with a plant’s time in the flora was Southwood’s work of 1961. Analysis showed a significant linear correlation in the number of insect herbivore species and the number of Quaternary fossil records of various British trees, with higher invertebrate species associations occurring with trees having long and abundant histories in the British flora (Southwood 1961). The
native conifer *Pinus sylvestris* was given a time in the British flora of 12,000 years and an association of 91 insect species, whereas a species of the introduced genus *Picea*, was present for just 500 years and had an insect community of some 37 species (Southwood 1961). The results however appeared clouded by the effect of vegetation area as well as length of time in the flora. More recent analysis of the data suggests recent abundance of the plant species is more important in determining its insect load than length of time it has spent in the flora (Claridge and Wilson 1978, Kennedy and Southwood 1984, Denno and Roderick 1991).

If planted area or abundance of a species is indeed more important than its time in the flora, then a species such as *Picea sitchensis* which has been in the British flora less than two hundred years, but is highly abundant, may be expected to have gathered an invertebrate community similar to that of a native coniferous species (*Pinus sylvestris*). Claridge and Evans (1990) found *Picea* (*P. abies* and *P. sitchensis*) to support just 90 herbivorous species; this is considerably lower than the figure of 178 phytophagous species on *Picea* from the Institute of Terrestrial Ecology’s phytophagous insect data bank (PIDB) (Welch 1986). For *Pinus* the Claridge and Evans (1990) figure is almost doubled to 172 species with a similar increase in numbers of species from the PIDB data to 263 phytophagous species (Welch 1986). This suggests that length of time is important to some extent, as *Picea* covers half again as much area as *Pinus*, 642,748 compared to 415,356 hectares (Claridge and Evans 1990), but still has fewer herbivore species, potentially limited by its time in the flora.
Although *Picea* species richness is lower than that of *P. sylvestris*, the introduced species has gained a considerable number of herbivorous species (53) between 1961 and 1990, the period separating the two research papers (Southwood 1961, Claridge and Evans 1990). This increase could be a result of better recording methods covering more insect orders in the later paper (Welch 1986) or be a result of an extension of invertebrate species ranges into *P. sitchensis* plantations. Fraser and Lawton (1994) have reported expansion of British moth species (*circa* 50 species) onto introduced conifer species in the UK, including *P. sitchensis*. Those species shifting tend to be generalist in their original lifestyle, feeding on a wide range of angiosperms, and tending to have original hosts of woody trees and shrubs (Fraser and Lawton 1994). However the native *P. sylvestris* still supports more lepidopteran species (56, PIDB) than introduced *Picea* (36, PIDB) (Welch 1986), so host range expansion onto introduced species has yet to catch up with the native complement. Pest species such as *Elatobium abietinum* have also extended their ranges from native European species such as *Picea abies* to introduced *P. sitchensis* (Straw 1995). *Picea sitchensis* is therefore in the process of gaining more invertebrate species and could foreseeably have a similar complement of invertebrates to *P. sylvestris* within the near future, a result of its present high abundance and its rapidly increasing time in the flora in terms of insect generations.

Other recently introduced tree species have also gained a complex herbivorous insect assemblage in the UK. *Acer pseudoplatanus* (Sycamore) showed the highest number of invertebrate species for the genus in the UK despite being in the flora for just 1800 years (Claridge and Wilson 1981), the species also supported unique species not found on the
more native *A. campestre*. The high levels of species richness on *A. pseudoplatanus* are accounted for by its present high abundance and its taxonomic relatedness to species present in the flora (Claridge and Wilson 1981), making extensions of invertebrate ranges onto it easier. Therefore an introduced tree species invertebrate community is a balance between its time in the flora, its abundance and taxonomic relatedness to other species already in the flora. These factors define the rapidity at which it gains its invertebrate community, particularly the herbivores.

5.1.2 Plant Chemistry.

Although there are many examples of species area accounting for high invertebrate diversity in plant species, the correlations often fail to account for more than 70% of the variance (Claridge and Wilson 1981, Kennedy and Southwood 1984), the remaining variance is thought to be due to factors such as plant chemistry, form and range. The length of time a plant has been in the flora also affects the ability of an invertebrate species to develop mechanisms, either physiological or behavioural, to overcome plant defence systems. This is especially the case for trees with high levels of secondary chemicals, such as the conifers. Plants are thought to produce secondary metabolites for a number of purposes including growth and developmental control, colour and scent attraction and as chemical defences against herbivory (Harborne 1997).

Secondary chemicals such as tannins, terpenoids (terpenes) and lignin are contained within plant tissue causing various undesirable effects when consumed by invertebrates.
Tannins associate with proteins in the gut of insects thereby reducing protein absorption and limiting invertebrate growth rates, whilst lignin, especially abundant in tree tissue, is tough and difficult to digest again slowing herbivory rates and growth (Speight and Wainhouse 1989). Terpenoids, abundant in coniferous species, cover a large range of substances based on the isoprene molecule; some are involved in growth and photosynthesis others performing a strictly secondary function (Cotton 1996).

Three major classes of the terpenoid molecule have been classified; the monoterpenoids, sesquiterpenoids and the triterpenoids (Harborne 1997), perhaps the most important of which in conifers are the monoterpenes. Monoterpenes or terpenes accumulate in the needles and bark, and are considered to have an anti-herbivory function although evidence is somewhat circumstantial, with monoterpenes acting as feeding attractants to some invertebrate species, especially aphids, silkworms and various pine beetles (Langstrom and Hellqvist 1993, Harborne 1997). However these are likely to be exceptional cases of evolutionary adaptation and monoterpenes are probably toxic or at least repellent to most invertebrates. Invertebrates will be attracted or repelled by different species of trees and by different individuals of the same species, due to slight variations in the monoterpenes being released at any given time. This results in variation in the invertebrate communities occurring on different conifer species because of adaptation to the species’ secondary chemicals.

The type, balances, quantities and positioning of defensive chemicals can result in changes in the invertebrate communities found on plant species, including the conifer
species under investigation. Defensive chemicals particularly affect the primary
consumers of the plant which in turn, due to either their presence or absence, secondarily
affect the populations of their predators. Other factors associated with the plant such as
physical structure and habitat will have more of an affect on the non-herbivorous aspect
of the invertebrate community.

Positioning of defensive chemicals affects the specific site of invertebrate feeding and the
damage caused (Hoy et al. 1998). Jack pine (Pinus banksiana) was found to have higher
water and nutrient levels in the distal portion of its needles, with monoterpane
concentration, particularly myrcene and limonene, also being high in the distal region
(Wallin and Raffa 1998). By concentrating its defensive chemicals in areas of high food
quality, the plant attempts to reduce its nutritional loss to the jack pine budworm
(Choristoneura pinus pinus) which feed in the basal area of the needles, themselves
attempting to balance exposure to defensive chemicals with adequate nutritional intake.
Defensive chemical levels also respond to invertebrate attack, levels increasing in
response to herbivory or bark damage. This is especially shown with monoterpenes in
conifers, increasing up to 100 fold in a week after bark beetle damage (Raffa 1991, Paine
et al. 1997), the level varying with tree species under investigation.

5.1.3 Plant Architecture.

As mentioned, the physical structure and the growth form of the two tree species are
different (Parker 1995) causing different habitat niches and feeding sites to be available
to invertebrate species. The architectural complexity of a plant is characterised by two factors, the size of the plant, and therefore the positioning of the plant tissue in space, and the number and variety of plant structures, i.e. the number, different types, form and persistence of structures like, branches, needles, leaves and trunks (Strong et al. 1984, Denno and Roderick 1991, Parker 1995). Large complex plants, such as trees, which are persistent, provide a greater number of stable microhabitats and are expected to have a greater diversity and abundance of invertebrates in general, and herbivores especially (Claridge and Wilson 1976, Lawton 1983, Strong et al. 1984, Denno and Roderick 1991).

The most extensively researched flora and fauna in the light of the association of plant architecture with invertebrate diversity is that of Britain, with results reported as ratios, factoring out plant abundance (Lawton and Schroder 1977, Lawton and Price 1979, Strong and Levin 1979, Lawton 1983). Trees have the richest fauna followed by bushes, herbs and monocotyledons, so the coniferous trees sampled during the present research should have a diverse invertebrate community compared to that of their understory. Differences in invertebrate communities are also reported with variations in the seasonality of the plant. Deciduous trees lose and then regain some of their structural complexity every year, with leaf fall and bud burst, resulting in a peak in faunal diversity during the summer months, whilst coniferous species support a similar level of structural complexity throughout the year by maintaining needles, resulting in a more consistent diversity of invertebrates throughout the year (Lawton 1983, Strong et al. 1984).
Size due to a plant's age should also have an effect on the invertebrate diversity, a young small sapling tree would be expected to have a less diverse and abundant community than a large mature tree, with species being accrued with developing age and complexity (Lawton 1983, Brown 1991). Saw-fly (Diprionidae) populations were lower in younger denser *P. sylvestris* plantations compared to older more open canopy sites, suggesting that *P. sylvestris* plantations should be maintained below the age of 40 years to reduce the risk of potentially damaging levels of saw-fly populations (Simandl 1992). However this pattern of increased diversity and density in mature trees may change as the trees become old with reduced canopy complexity and density leading to reduced invertebrate diversity and density (Parker 1995). Evidence has been found for such a reduction in some densities of taxa on older plantation trees and a change in the guild dominating the community. For example herbivore biomass was found to be higher in young coniferous forests compared to old, with the young trees' community dominated by the sap-sucking guild, unlike defoliator domination in the older trees (Schowalter *et al.* 1988, Schowalter 1989, Simandl 1993). Seven arthropod orders in medium aged (40 years) *P. sylvestris* monoculture plantations showed preference and high densities for this age category than older (>80 years) trees with less dense canopies (Simandl 1993), the invertebrates responding to the reduction in the canopy density. However other research has found similar abundances of invertebrates in young (10-15 years) and established (25 years) conifer species in the UK, despite the younger trees having smaller canopies (Ozanne 1991). Here younger trees supported higher foliar densities enabling them to support as many invertebrates as the larger older trees with less canopy. It therefore appears that age
per se cannot account for invertebrate diversity and that the latter is simply a reflection of the structural diversity of a plant and the complexity of its chemical defence.

As well as the overall complexity of a tree and its general large size, the finer details of its structural complexity also impact on the invertebrate communities found. Variation in the quantity of canopy, branch density, twig development and leaf structure and quantity will alter habitat structure and complexity for invertebrates. *Pinus sylvestris* and *Picea sitchensis* show distinct patterns in their branch and needle growth. Plantation *P. sylvestris* has relatively high inter-whorl and inter-nodal (branch) distances with fewer nodes per branch compared to *P. sitchensis* (Ozanne 1991). Height to base of green canopy is greater than that for *P. sitchensis* (Ozanne 1991), resulting in a canopy of more separate branches, low lateral growth and narrower canopy depth. *Picea sitchensis* with its high number of branches each with high numbers of nodes, and lower height for start of green canopy (Ozanne 1991), has a dense and more crowded canopy structure, providing many more microhabitats for invertebrates. This is reflected in the leaf area index (LAI, m² m⁻²), the ration of the total one-sided leaf area to the projected ground area, and the leaf area density (LAD m² m⁻³), the mean leaf area per unit volume (Parker 1995). Coniferous species have higher LAI and LAD compared to broadleaf trees, 15-20 compared to 7-12, and 0.3-0.7 compared to 0.2-0.5 respectively (Parker 1995), showing conifers to have denser canopies and more needles/leaves than deciduous species.

Many invertebrates specifically require either a dense or open habitat in which to live, this is particularly true of the Araneae which require very specific and varying habitat
structures in which to hunt and build their webs (Gunnarsson 1988). Araneae abundance is reduced with loss of canopy structural complexity after forest clearance (Watt et al. 1997). Thomisidae, a family of raptorial spiders and the Theridiidae, scaffold-building species, seem to prefer conifer branches with high needle density, e.g. *P. sitchensis*, providing cover for hunting or complex structure for web construction (Gunnarsson 1988, Ozanne 1991). Whereas sheetweb-building spiders (Linyphiidae) prefer areas with lower needle density and higher percentages of twigs, providing more open sites for web construction (Gunnarsson 1988). Those species considered tourist which are often moving through the habitat or using it to rest might also be expected to be associated with trees with more open canopies, such as the pines, with larger inter-branch spaces through which they can travel.

This increased complexity of the *P. sitchensis* canopy is not restricted to the branch level, as needle structure and arrangement also differ between the two species. *Pinus sylvestris* has long thin (4cm) needles set in pairs which occur in lower densities on the branches than the tough short and dense needles of *P. sitchensis* (Ozanne 1991). It therefore appears that *P. sitchensis* has a denser and more needle-rich fine structure than *P. sylvestris* which could be reflected in considerable differences in the invertebrate community between the two species, especially for those species which are particularly structurally or needle-quality dependent. An aspect of needle-quality is their age and palatability, age and quality of needles present in a canopy affect *Cinara pinea*, the large pine aphid. It was found to be more abundant in *P. sylvestris* canopies on shoots, which were thinner and had phloem vessels relatively near the surface (Kidd and Tozer 1985).
Different age classes of aphids also feed in different areas of the shoots, attempting to balance nutritional intake, small aphids feeding near the shoot tips (buds), with cryptic anti-predatory behaviour, larger aphids feeding further back on the shoots amongst the needles, where they are less visible to avian predators (Kidd and Tozer 1985, Larsson 1985).

5.1.4 Canopy Microclimate.

An extension of plant structure as an influencing factor on invertebrates, is the variation in microclimate that results from variation in the plants' physical structure at the branch, tree, plantation and regional level. The fine structure at the branch level and its microclimate have already been shown to have effects on the positioning and species present on trees, such as the distribution of *Cinara pinea* (Kidd and Tozer 1985, Larsson 1985) and the numbers of large spiders on branches with high needle density and therefore higher humidity (Gunnarsson 1988). Other taxa show similar variation due to microclimate in tree canopies including the Collembola and Acarina. Collembola are particularly microclimate sensitive. With their longevity decreased in dry atmospheres, they actively seek moist areas and have been shown to climb into the canopy to seek moist conditions, particularly after rainfall (Lambert 1970, Bowden *et al.* 1976). Particular species of Collembola have also been shown to prefer particular tree species due to the microhabitats (bark type) and microclimate they provide (Prinzing 1997, Hopkin 1998), with *Entomobrya nivalis* being more abundant on pines than beeches and
Anurophorus laricis having low abundances on pine due to the dry habitat (Lambert 1970).

Canopy mites (Acarina), an often forgotten and highly abundant and diverse aspect of the canopy community (Walter and O’Dowd 1995, Winchester 1997b, Walter and Behan-Pelletier 1999), are particularly responsive to the structural diversity of the canopy and its microclimate. Responding to bark type, leaf structure, epiphyte load and microclimate characteristics (Walter and Behan-Pelletier 1999), abundance and diversity being greater on more structurally complex leaves, with highly sculptured cuticles (Walter and O’Dowd 1995). Considerable taxonomic radiation is thought to have occurred in the Acarina to fill the canopy microhabitat conditions of old growth Picea sitchensis, particularly the deep, 4-28 cm, moss mats associated with the branches (Winchester 1997b). Many Acarina species are also recorded as host-specific, especially those feeding on lichens, being closely associated with specific lichen species, themselves responding to specific microclimatic conditions (Walter and Behan-Pelletier 1999). More of these lichen specific species may be expected in P. sitchensis due to its high, dead, organic matter content and increased epiphyte load (Ford 1985). Therefore, due to the variation in their microclimate which results from differences in their physical structure, the two tree species should support very different invertebrate communities, particularly in some sensitive taxa.

The larger scale structure of the two conifer plantation types will also have an effect on the invertebrates, with the more open canopy of P. sylvestris providing lower humidity,
higher temperature, greater through-radiation and inter-trunk wind speed conditions than \textit{P. sitchensis} plantations. Insect species comprising larger individuals are more likely to be affected by these variations in tree structure. Increased levels of shade in conifer plantation woodland rides have been shown to have a negative effect on the species richness and abundance of Heteroptera and Coleoptera (Greatorex-Davies \textit{et al.} 1994), a result of direct shading and indirect effects on the host plants of the Heteroptera. This pattern in the understory species richness could have a knock-on effect on the canopy invertebrate community in the shady \textit{P. sitchensis} if there is some movement between the understory and canopy community. The pattern will also be accentuated in the core regions of plantations due to the lower light intensity levels away from plantation edges.

5.1.5 Regional Climate.

At the greatest scale the regional climate may have an effect on invertebrate species occurring in plantation forests. The two tree species under investigation vary considerably in their planting regions, limiting the ability of some invertebrate species to inhabit them. \textit{Pinus sylvestris} although native to Scotland is planted in southern and eastern regions, with the present research sites located in North Yorkshire, whereas \textit{P. sitchensis} is more abundantly planted in the north with the research sites in Northumberland. Overall variation in regional climate limits the range of some invertebrate species which, being ill-adapted to the conditions at sites in either the south or north, may not occur there in tree species they would otherwise be expected to inhabit. They are outside their climatic range. The limitations of invertebrate ranges inside the
range of their host species is often a result of climatic conditions affecting generation times or predation rates. *Ladoga camilla*, the white admiral butterfly feeds on the ubiquitous honeysuckle (*Lonicera periclymenum*), however the butterfly is restricted to Southeast England (Strong *et al.* 1984). Low temperatures in other regions of the UK are thought to slow larval development enough to significantly increase bird predation rates of the caterpillar leading to un-viable population levels (Strong *et al.* 1984). In a similar fashion the thimbleberry aphid (*Masonaphis maxima*) is restricted to a very small percentage of its host plant range, as climate in the other regions provides too short a time to achieve the three generations per year necessary to maintain population levels (Strong *et al.* 1984). These regional and global climate effects if changed could lead to considerable shifts in the invertebrate communities present in areas. Global warming has been predicted to advance budburst in *P. sitchensis* by 5-7 days, extending the period available for some pest species, such as *Elatobium abietinum*, to establish damaging population levels (Straw 1995). This could result in increased regularity of severe pest outbreaks and a shift in the overall invertebrate community, some species potentially being out-competed, although earlier development of predator populations could balance the outbreak effect.

Comparison of the invertebrates collected in *P. sylvestris* and *P. sitchensis* will be made to establish whether invertebrate species, richness, density and guild composition follow or contradict any of the expected patterns suggested by previous research, in the UK plantation forests. Particular focus will be placed on the Acarina, Araneae, Collembola
and phytophages all of which have previously been shown to respond specifically to the structure and climate of the habitat in which they are found.
5.2 Methods.

Differences between the edge and core invertebrate communities of each tree species were explored in the edge-effect chapter highlighting the importance of the edge habitat in *P. sitchensis* and core habitat in *P. sylvestris*. A comparison of the edge or core habitat in each tree species would reflect the different response to edge proximity (discussed in Chapter 3) rather than a true reflection of the differences between the whole invertebrate community of the two tree species. Therefore in the invertebrate analysis the data from both edge and core areas (all samples) were combined to explore the variation in invertebrate communities due to tree species alone, as no single area of a plantation patch can be considered to be completely representative of the whole community.

Although the use of transects means the sampling scheme is non random, when comparing the two tree species, the samples equally represent the two invertebrate communities caused by edge proximity and therefore are useful in highlighting the basic differences between the two tree species. For the *P. sylvestris* data set all 48 samples from the three transects were used, *P. sitchensis* data included the samples from four transects excluding the edge and core block data sets. Differences in the abiotic conditions, total invertebrate and order level densities, species richness and guild composition were explored, also differences between the particular species present.

Temperature (°C) and relative humidity (%) mean values were calculated from the samples taken in each of the two tree species and analysed using independent sample t-
tests. In conjunction with this invertebrate mean density, species richness and taxa lists were compared between the two tree species. Mean density per m\(^2\) ground area for total invertebrate capture and individual taxa were calculated in each tree species and analysed with independent sample t-tests. In a similar way total invertebrate richness and species richness within taxa for those identified further than order (Acarina, Araneae, Coleoptera and Collembola) were compared between the two tree species.

Abundance of invertebrate orders as a percentage of total invertebrate capture were calculated to highlight any variation in the contribution specific orders made to the community in each of the two tree species. Acarina, Araneae, Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Psocoptera and ‘other’ (combined category of all orders represented by just one or two individuals) had percentage abundance calculated for the combined transect data in each tree species and expressed as a percentage of the total invertebrate capture for the respective tree species. These were represented as pie charts for visual comparison.

Order, family, genus and species level comparison of invertebrate communities occurring in the two tree species was performed using species lists of those orders identified to lower taxonomic levels, specifically the Acarina, Araneae, Coleoptera and Collembola. The aim was to establish whether invertebrate species occurred in a particular tree species, or if any unusual species were captured out of their normal range or were new records for the area/habitat.
Finally the invertebrates were classified into functional guilds (see Chapter 2, Table 2.2), with the guild data being analysed in a similar way to the invertebrate data, with mean density (per m² ground area) calculated for each guild for each tree species and compared using independent sample t-tests. Taxon richness within each guild was calculated and compared with the same guild in the other tree species. Percentage contribution of each of the guilds to total capture rates was calculated for combined tree species data, presented as pi charts for comparison of guild structure in the two tree species. Further more detailed guild analysis was possible using the Coleoptera and Acarina species richness, and percentage contribution to the total order was calculated for the Coleoptera and Acarina guilds and compared between tree species. Differences in the composition of the guilds between the two tree species at the order, family, genus and species level were explored and discussed. Mean predator/prey ratio was also compared between the two species.
5.3 Results.

5.3.1 Abiotic Data.

Although the abiotic data readings from *Pinus sylvestris* and *P. sitchensis* followed a similar reduction in temperature (1°C) and increase in relative humidity (5%) with distance from edge (Chapter 3), *P. sylvestris* appeared to have on average higher temperature and lower humidity readings when compared to *Picea sitchensis*, which would be expected. Mean temperature being approximately 14.7°C and humidity 86% in *P. sitchensis* compared to 19°C and 67% respectively in *P. sylvestris*. However the differences were not significant and only limited conclusions could have been drawn from the analysis as abiotic readings were collected on different days, in different years and indeed from different regions of the UK for each of the two tree species. Therefore the likelihood was that any differences were due to diurnal, annual and regional variations in abiotic conditions rather than any difference between the two tree species.

5.3.2 Mean Densities.

Mean total invertebrate density across all *P. sitchensis* samples was 908.36 invertebrates per m², with a *P. sylvestris* density of 428.64 m², under half the number of invertebrates recorded in the *P. sitchensis* samples (Table 5.1). Although this may suggest higher invertebrate densities in *P. sitchensis*, the difference was not significant (P > 0.2), both tree species, in these plantation areas supporting a similar number of canopy invertebrates.
per m² ground area. Further independent sample t-tests were performed on the mean invertebrate density data across all transects for those taxa with high abundances, including the Acarina, Araneae, Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Psocoptera (Table 5.1). Taxa with low densities, just a few individuals per transect were excluded, preventing unreliable statistical analysis. Only one significant result was obtained from all nine orders, the Lepidoptera showed significantly higher densities per m² ground area in *P. sylvestris* (Figure 5.1).

Two further taxa showed a trend towards a significant difference in mean density per m² between the two tree species. Acarina showed higher mean densities per m² in the *P. sitchensis* samples which was unsurprising because of the high quantity of standing dead organic matter and high fungal/lichen communities present in *P. sitchensis* canopies (Ford 1985), providing food, hunting sites, and a diversity of microhabitats. The Collembola also showed higher densities in the *P. sitchensis* samples, although not significantly so.

**5.3.3 Mean Species Richness.**

Comparison of mean species richness between the two tree species by independent samples t-test was performed on total invertebrate richness and from the five orders for which species richness was calculated (Acarina, Araneae, Coleoptera and Collembola), just two significant results were obtained (Table 5.2).
Table 5.1. Independent sample t-test results comparing mean densities (m$^2$) of invertebrate taxon between *Picea sitchensis* and *Pinus sylvestris* plantations.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Mean Density (m$^2$)</th>
<th>P. sitchensis</th>
<th>P. sylvestris</th>
<th>P Value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>P. sitchensis</td>
<td>P. sylvestris</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total invertebrate</td>
<td>908.37 (SE± 265.35)</td>
<td>428.64 (SE± 181.53)</td>
<td>0.23</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Acarina</td>
<td>311.76 (SE± 92.35)</td>
<td>48.35 (SE± 27.21)</td>
<td>0.06</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Araneae</td>
<td>4.94 (SE± 1.25)</td>
<td>11.17 (SE± 3.57)</td>
<td>0.12</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Coleoptera</td>
<td>12.83 (SE± 2.04)</td>
<td>14.75 (SE± 4.99)</td>
<td>0.71</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Collembola</td>
<td>121.51 (SE± 53.24)</td>
<td>15.1 (SE± 6.24)</td>
<td>0.15</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Diptera</td>
<td>49.54 (SE± 16.39)</td>
<td>24.73 (SE± 4.36)</td>
<td>0.26</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Hemiptera</td>
<td>195.37 (SE± 109.15)</td>
<td>63.96 (SE± 17.91)</td>
<td>0.36</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>29.24 (SE± 12.34)</td>
<td>22.94 (SE± 8.48)</td>
<td>0.71</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>1.05 (SE± 0.39)</td>
<td>8.52 (SE± 3.04)</td>
<td>0.03</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Psocoptera</td>
<td>184.08 (SE± 124.37)</td>
<td>198.85 (SE± 154.65)</td>
<td>0.94</td>
<td>NS</td>
<td></td>
</tr>
</tbody>
</table>

SE = Standard error of the mean, NS = non significance, * = P< 0.05.
Mean density (n×) (+- 2 SE)

Pinus sylvestris samples (F= < 0.05 indep. t-test).

Tree species

Pinus sylvestris  Picea sitchensis

Mean density (m²⁻¹) (+- 2 SE)
Table 5.2. Independent samples t-test results comparing mean species richness of invertebrate taxa between *Picea sitchensis* and *Pinus sylvestris* plantations.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Mean Species Richness</th>
<th>P Value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>P. sitchensis</em></td>
<td><em>P. sylvestris</em></td>
<td></td>
</tr>
<tr>
<td>Total invertebrate</td>
<td>33.5 (SE± 2.6)</td>
<td>49 (SE± 6.11)</td>
<td>0.04 *</td>
</tr>
<tr>
<td>Acarina</td>
<td>6.75 (SE± 0.85)</td>
<td>6.67 (SE± 0.67)</td>
<td>0.95 NS</td>
</tr>
<tr>
<td>Araneae</td>
<td>6.75 (SE± 1.7)</td>
<td>14 (SE± 4.51)</td>
<td>0.15 NS</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>5.5 (SE± 0.87)</td>
<td>15 (SE± 1.15)</td>
<td>0.001 ***</td>
</tr>
<tr>
<td>Collembola</td>
<td>3.5 (SE± 0.29)</td>
<td>3 (SE± 0.58)</td>
<td>0.44 NS</td>
</tr>
</tbody>
</table>

SE = Standard error of the mean, NS = non significance, * = P< 0.05, *** = P< 0.001.
Figure 5.3. Mean coleopteran species richness (m$^2$) between *Picea sitchensis* and *Pinus sylvestris* samples (*P* = 0.001).
Total invertebrate richness was higher (P<0.05) in *P. sylvestris*, with a mean of 49 species (Figure 5.2), this increased richness was due to higher species richness of Araneae (not significant) and Coleoptera. Other less common orders also appeared more frequently or solely in *P. sylvestris* than *P. sitchensis*, such as the Ephemeroptera and Trichoptera (discussed below).

Coleoptera was the only taxon showing a significant difference in its mean species richness, being 3 times higher in *P. sylvestris* (Figure 5.3). The latter supported 14 families, with a minimum of 22 species, and particularly high numbers of Coccinellidae species, 7, (Table 5.5), whilst *P. sitchensis* had 7 families with a minimum of 10 species and 3 Coccinellidae species. *P. sylvestris* appears to be providing a considerably more diverse habitat for the Coleoptera species. Although not significant, the Araneae showed a trend towards increased species richness in the *P. sylvestris* samples, with a mean species richness over twice that of *P. sitchensis* (Table 5.2). Families such as Araneidae, Clubionidae, Tetragnathidae, Theridiidae and Thomisidae showed particularly high richness (Table 5.4).

5.3.4 Invertebrate Species.

Although significant results in the mean densities and species richness analysis of the two tree species were few, there were considerable differences in the actual invertebrates occurring with the two tree species. Densities and species richness values of certain taxa appeared similar between the two tree species, however the actual species composition
varied for some orders. The greatest variation in community composition was seen in the Acarina, Araneae and Coleoptera, with less dramatic variations for some other taxa.

Interestingly there were no differences in the species of Collembola present in the two tree species with all four, *Anurophorus laricis, Entomobrya nivalis, Lepidocyrtus curvicollis* and *Sminthurus fuscus* occurring in both. Throughout the present analysis Collembola have responded in various ways to alterations in the canopy habitat, particularly edge proximity, however these invertebrates fail to respond at the species level to the tree species they occur in.

Four orders showed specific preference for one or other of the tree species, the Pseudoscorpions recorded solely in the *P. sitchensis* samples, the canopy of this tree species providing particularly suitable habitat for these small predatory organisms, with stable abiotic conditions and ample food supply. In contrast Trichoptera, Ephemeroptera and Mecoptera occurred solely in the *P. sylvestris* data set, these are tourist orders which are weak fliers preferring open but shady habitats.

5.3.4.1 Acarina.

*Picea sitchensis* and *Pinus sylvestris* showed specific species complements of Acarina, both tree species having nine species of mite, six of which were shared, with a further three species being unique to each (Table 5.3). The shared species were common and occurred in high densities particularly the Prostigmata, *Anystis sp.* and *Bedella sp.* and the
Oribatida *Camisia sp.* and *Chamobates sp.*, with the three additional species in each tree species occurring in low densities. Species *Pergamasus sp.* (Mesostigmata), *Belba sp.* and *Platynothurus sp.* (Oribatida) occurred only in *P. sitchensis*, which could be a regional, abiotic, or microhabitat response of these species to the conditions provided by this tree species. In *Pinus sylvestris* the Oribatida species *Carabodes sp.*, *Cepheus sp.* and *Cymbaeremaeus sp.* occurred in low densities with just one individual of *Cepheus sp.*, however *Cymbaeremaeus sp.* occurred in relatively high densities but mainly in *Pinus sylvestris* patch 3.

5.3.4.2 Araneae.

Although spider density and species richness were not significantly different between the two tree species, *P. sylvestris* appeared to have more species and to some extent a different complement of species to *P. sitchensis* (Table 5.4). Four spider families the Araneidae, Clubionidae, Tetragnathidae and Thomisidae were unique to the *P. sylvestris* samples. Just three spider families were represented in the *P. sitchensis* samples, all of which also occurred to some extent in the *P. sylvestr* samples, the Linyphiidae, Metidae and Theridiidae (Table 5.4). Four species of Linyphiidae, *Drapetisca socialis*, *Leptophantes expunctus*, *L. tenuis* and *Linyphia triangularis* occurred in the *P. sylvestris* samples, with *L. tenuis* being unique to the tree species. Whereas nine species occur in *P. sitchensis*, six of which are unique to the samples (*Bolyphantes luteolus*, *Leptophantes alacris*, *L. obscurus*, *L. zimmermanni*, *Pelecopsis nemoralis* and *Pityohyphantes phrygianus*).
Table 5.3. Acarina order and species list for *Picea sitchensis* and *Pinus sylvestris* samples.

<table>
<thead>
<tr>
<th></th>
<th><em>Picea sitchensis</em></th>
<th><em>Pinus sylvestris</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mesostigmata</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Pergamasus sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Oribatida</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Belha sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Camisia sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Carabodes sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Cepheus sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Ceratoppia sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Chamobates sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Cymbaeremaeus sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Platynothrus sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Prostigmata</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Anystis sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Bedella sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Leptus sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

+= presence
Table 5.4. Araneae family and species lists for *Picea sitchensis* and *Pinus sylvestris* samples.

<table>
<thead>
<tr>
<th>Araneidae</th>
<th>Picea sitchensis</th>
<th>Pinus sylvestris</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Araneus diadematus</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Araniella sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Atea sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Cyclosa conica</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Gibbaranea gibbosa</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Nuctenea umbratica</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Zygiella sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Clubionidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Clubiona sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Linyphiidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Bolyphantes luteolus</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Drapetisca socialis</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Leptophantes alacris</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Leptophantes expunctus</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Leptophantes obscurus</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Leptophantes tenuis</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Leptophantes zimmermanni</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Linyphia triangularis</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Pelecopsis nemoralis</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Pityohyphantes phrygianus</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Metidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Metellina sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Metellina mengei</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Tetragnathidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Tetragnatha extensa / pinicola</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Tetragnatha montana / nigrita / obtusa</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Theridiidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Achaearanea sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Anelosimus vittatus</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Theridion sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Theridion mystaceum / melanurum</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Theridion pallens</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Theridion tinctum</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Thomisidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Philodromus sp.</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Philodromus praedatus</em></td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

*sp. = species, + = presence*
Table 5.5. Coleoptera family and species lists for *Picea sitchensis* and *Pinus sylvestris* samples.

<table>
<thead>
<tr>
<th>Family</th>
<th><em>Picea sitchensis</em></th>
<th><em>Pinus sylvestris</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Cantharidae</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Carabidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Dromius quadrimaculatus</em></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Chrysomelidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Cleridae</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Coccinellidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Adalia sp.</em></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Adalia bipunctata</em></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Adalia 10-punctata var.</em></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Anatis ocellata</em></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Aphidecta obliterata</em></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Calvia 14-gultata</em></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Coccinella 7-punctata</em></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Propylea 14-punctata</em></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Cryptophagidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Curculionidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Elateridae</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Lathridiidae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Melandryidae</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Nitidulidae</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Salpingidae</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Scolytidae</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Staphylinidae</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

*sp.* = species, + = presence
Mean density (m²) for Pinus sylvestris and Picea sitchensis samples.
Identification of Coleoptera was performed to family, with the Coccinellidae taken to species, a total of 14 families and eight Coccinellidae species being recorded in the two tree species. *P. sitchensis* shared all 7 recorded families with *P. sylvestris* (Table 5.5), with just one of the three Coccinellidae species being unique to *P. sitchensis* (*Aphidecta obliterata*). Although a high number of families were recorded in the two tree species on average, mean densities of each were low, with just one or two examples of each family in the whole data set (Figure 5.4). Those families showing higher densities occurred in one or other of the tree species, Carabidae and Chrysomelidae having high densities in *P. sylvestris* and Staphylinidae having high densities in *P. sitchensis* (Figure 5.4). Only one family the Coccinellidae occurred in high densities in both tree species (Figure 5.4).

The seven families found in both tree species (being the sole families in *P. sitchensis*), were Carabidae, Chrysomelidae, Coccinellidae, Cryptophagidae, Curculionidae, Lathridiidae and Staphylinidae, these families show a range of lifestyles and habitat preferences. The Carabidae or ground beetles showed higher densities in *P. sylvestris* compared to *P. sitchensis* (Figure 5.4), although predominantly ground taxa many species do hunt for prey in vegetation canopies. In the same way more leaf beetles (Chrysomelidae) were found in *P. sylvestris* (Figure 5.4), Chrysomelidae species are host-specific feeding on living plant tissue. Three further families found in both tree species but showing low densities were the Cryptophagidae, Curculionidae and Lathridiidae. Curculionidae are the plant feeding weevils while the other two families are
scavengers of decaying material. Many species in these families are considered tree species living on or under bark, therefore higher densities were to be expected.

Staphylinidae were one of the three families that showed higher densities in *P. sitchensis*, these are predominantly active predatory beetles that hunt in areas of high food density. Coccinellidae were the most abundant beetles in both tree species making up a considerable proportion of the predatory guild in both, seven species occurred in *P. sylvestris* with just three in *P. sitchensis*. The following two species are of particular note. *Anatis ocellata* is a known conifer species occurring solely in *P. sylvestris*, being particularly adapted to the conditions and food sources provided by these tree species. The only species to occur solely on *P. sitchensis* was *Aphidecta obliterata*, the larch ladybird, this species is normally associated with fir trees but appears to be spreading its range onto the large areas of plantation *P. sitchensis*.

Of the seven families which were confined to the *P. sylvestris* samples most are predatory occurring in low densities (Figure 5.4), some particularly specialise in feeding on the invertebrate visitors to flowers and are therefore likely to be using the canopy as a resting site before feeding in the understory. The Scolytidae are of particular interest, these are the bark beetles, which burrow under the bark of specific tree species. Due to this lifestyle one would expect few individuals to be captured by the pyrethrin knockdown technique, therefore a reasonable population must be occurring in *P. sylvestris* with a few moving above the bark and being captured by the technique. Associated with this family were their specific predators the Cleridae and Melandryidae (Figure 5.4) which have
some species which specialise in feeding on bark beetles, thus a bark beetle and associated predator community is developing in the *P. sylvestris* plantations but not in those of *P. sitchensis*.

5.3.5 Invertebrate Percentage Abundances.

Calculation of the percentage abundance of key invertebrates to total invertebrate capture was performed by tree species. Visual comparison of total invertebrate percentage abundance for each tree species from the pi charts showed clear differences in the proportional composition of the invertebrate communities (Figures 5.5 a and b). *Picea sitchensis* showed a community dominated numerically by 4 orders (Figure 5.5a), the Acarina, Collembola, Hemiptera and Psocoptera, all other orders showing relatively low percentage contribution to the overall community, particularly the ‘other’ category. The domination of just four orders and low ‘other’ percentage highlights the lack of unusual species in *Picea sitchensis* resulting in its significantly lower species richness (Table 5.2). In contrast the *Pinus sylvestris* data had a more equal community pattern, with domination by just one order, the Psocoptera. Aside from the Psocoptera all orders showed relatively consistent percentage contributions to the community, including the ‘others’ category, which highlights the incidence of greater numbers of the more unusual orders and species within *P. sylvestris*, with less concentration on the detritus-living aspect of the community, as seen in *P. sitchensis*. 
5.3.6 Guilds.

Guild mean densities between tree species showed considerably more significant differences than invertebrate densities, with five significantly different densities four of which were higher in *P. sitchensis* (Table 5.7). The detritivore/fungivore, herbivore, predatory and scavenger guilds had significantly higher densities in *P. sitchensis* with just the tourist guild having higher densities in *P. sylvestris*. Although there were significant differences in the densities of different guilds between the two tree species their percentage contribution to the community was less dramatically different between the tree species (Figure 5.6). Percentage contributions of the guilds were similar between the species except for the contribution of the tourist guild, which appears to be more important in *P. sylvestris*. Along with these differences there was a significant difference in the predator/prey ratio value between the two tree species. *P. sitchensis* had a significantly higher (P=0.013) mean ratio value (0.27) than *P. sylvestris* (0.20), implying that *P. sitchensis* in general has a higher number of predators to prey within its invertebrate canopy community.

Further more detailed guild analysis for those orders identified beyond order and showing different guild strategies within their order (Acarina and Coleoptera) resulted in more significant results. Significant differences were seen between the detritivore and predatory guilds of Acarina between the tree species, both guilds having significantly (P=0.000) higher densities (146.78 and 96.02 respectively) in *P. sitchensis* than *P. sylvestris* (42.63 and 5.5 respectively). The pattern was continued in the percentage
orders for combined *Picea sitchensis* (A) and *Pinus sylvestris* (B) samples.
Table 5.6. Independent sample t-test results comparing mean densities (m²) of invertebrate guilds between *Picea sitchensis* and *Pinus sylvestris* plantations.

<table>
<thead>
<tr>
<th>Guilds</th>
<th>Mean Density (m²)</th>
<th>P. sitchensis</th>
<th>P. sylvestris</th>
<th>P Value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Detritivores /</td>
<td>491.80</td>
<td>256.42</td>
<td></td>
<td>0.001</td>
<td>**</td>
</tr>
<tr>
<td>Fungivores</td>
<td>(SE ± 42.26)</td>
<td>(SE ± 58.45)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herbivores</td>
<td>191.70</td>
<td>67.15</td>
<td></td>
<td>0.000</td>
<td>***</td>
</tr>
<tr>
<td>Parasitoids</td>
<td>29.04</td>
<td>22.94</td>
<td></td>
<td>0.317</td>
<td>NS</td>
</tr>
<tr>
<td>Predators</td>
<td>104.42</td>
<td>36.73</td>
<td></td>
<td>0.000</td>
<td>***</td>
</tr>
<tr>
<td>Scavengers</td>
<td>50.42</td>
<td>31.77</td>
<td></td>
<td>0.016</td>
<td>*</td>
</tr>
<tr>
<td>Tourists #</td>
<td>1.06</td>
<td>9.02</td>
<td></td>
<td>0.000</td>
<td>***</td>
</tr>
</tbody>
</table>

SE = Standard error of the mean, NS = non significance, * = P< 0.05, ** = P< 0.01 and *** = P<0.001.

# = only guild showing higher densities in *Pinus sylvestris*.
contribution pi charts (Figure 5.7) for the predatory guild which contributed a larger proportion of the community in *P. sitchensis* than *P. sylvestris*, the guild also having greater species richness in *P. sitchensis* (Figure 5.8).

The Coleoptera showed greater differences in the guild percentages with the *P. sitchensis* samples being dominated by the predatory guild whilst *P. sylvestris* had a more diverse coleopteran guild community dominated by predators, herbivores and detritivores. Few significant results were reported from the analysis of coleopteran guild species richness between the two tree species with just the herbivores showing higher species richness in *P. sylvestris* compared to *P. sitchensis* (Figure 5.9).
Tourists
Scavengers
Predators
Parasites
Herbivores
Detritivores

A

Tourists
Scavengers
Predators
Parasites
Herbivores
Detritivores

B
Detritivores

Predators

Detritivores

Predators

Detritivores

Pinus sylvestris (B) samples.
Figure 5.9. Mean coleopteran herbivore species richness ($m^3$) between *Pinus sylvestris* and *Picea sitchensis* samples ($P=<0.000$ indep. t-test).
Pinus sylvestris (B) samples.

A

Scavengers    Herbivores

Predators

B

Tourists
Scavengers

Detritivores

Predators    Herbivores
Invertebrate communities and guilds showed significant differences in their mean densities, species richness, species lists and their contribution to the community between the two conifer species over and above the variations found due to edge-effects. In general \textit{P. sylvestris} showed a less dense but more species rich invertebrate community than \textit{P. sitchensis}, this supports the expected responses in the invertebrate community to differences in the trees’ length of time in the flora, present land area coverage and structural and chemical properties. Abiotic conditions showed no significant differences between tree species, due to the high inter-transect variation in the data although a trend towards warmer and less moist conditions in \textit{P. sylvestris} was seen. Temperature appeared to be 4°C higher and humidity 15% lower in \textit{P. sylvestris}, a result of the more open canopy structure of the species (Ford 1985) allowing more radiation and air currents through to the lower canopy where readings were taken. These abiotic conditions favour larger invertebrate species capable of maintaining homeostatic balance in extreme conditions, rather than small soft bodied species dependent on moist surrounding conditions (present in \textit{P. sitchensis}), also more transient species such as tourists from open grassland areas favour the warm open habitat within \textit{P. sylvestris}.

5.4.1 Mean Densities.

Few significant differences were seen in mean density comparisons between the two tree species, with Lepidoptera the only order showing significantly higher densities in \textit{P.}
sylvestris (Table 5.1). However other trends (non-significant) were apparent, with higher densities of Acarina and Collembola in *P. sitchensis*, and overall greater invertebrate density in *P. sitchensis*. A trend towards higher total invertebrate density per m² ground area in *P. sitchensis* plantations concurs with previous findings in the UK. Twice the density of canopy arthropods were reported in *P. sitchensis* compared to *P. sylvestris* and *Pinus nigra maritima* by Ozanne (1991), with a mean of 1742.5 arthropods per m² ground area and 674.18 respectively. The higher density of arthropods in *P. sitchensis* were found to be insignificant when arachnid data were excluded, higher densities accounted for by the Araneae, Opiliones and Acarina (Ozanne 1991). Figures of mean arthropod densities were lower in the present study but still biased towards *P. sitchensis* plantations, 908.37 and 428.64 invertebrates per m² ground area for *P. sitchensis* and *P. sylvestris* respectively (Table 5.1).

Lepidoptera was the only taxon to show a significant difference in mean density between the two conifer species, being more abundant in *P. sylvestris* (Figure 5.1). Adult Lepidoptera are often considered tourists in the canopy community, using it as a temporary habitat, whilst away from their more common habitat of forest edges and understory (Warren 1991), although some micro species do feed in conifers (Fraser and Lawton 1994). Ozanne (1996) found a significant difference in the mean number of canopy Lepidoptera, per m² ground area between *P. sitchensis* and *P. sylvestris*, the spruce supporting greater numbers. However, *P. sylvestris* was reported to support more species than *Picea*, 23 compared to 9 (Young 1986), indeed *P. sylvestris* had a species richness per m² ground area of 0.75 compared to 0.5 for *P. sitchensis* (Ozanne 1996). The
increased densities found in *P. sylvestris* contradict previous findings a result of the increased complexity of the understory and the milder more open structure of the canopy, encouraging tourist populations of Lepidoptera.

The increased density of invertebrates in *P. sitchensis* is a result of a number of factors associated with the tree species, as discussed in the introduction, with the increased abundances of standing dead organic matter, high structural complexity and large epiphyte communities reported in *P. sitchensis*, all encouraging high invertebrate densities (Strong *et al.* 1984, Denno and Roderick 1991, Ozanne 1991, Pettersson *et al.* 1995, Esseen *et al.* 1996). However unlike previous research (Ozanne 1991) the Araneae seem not to be so important in the *P. sitchensis* data, showing a trend towards higher densities in *P. sylvestris* (Table 5.1). These higher densities of Araneae in *P. sylvestris* are likely to be associated with the high species richness in the Araneae also found in *P. sylvestris* (see below), the spiders occupying many more niches resulting in less intra-order competition enabling higher overall densities of the order. Whereas the Araneae in *P. sitchensis* support a few Araneae species with similar hunting techniques increasing competition for food resources resulting in restrictions in their overall densities.

There was a higher mean density of Acarina and Collembola in *P. sitchensis* (Table 5.1). Acarina and Collembola have been reported as important taxa in canopy communities with high diversities, densities and percentage contribution to the community (Bowden *et al.* 1976, Andre 1985, Stubbs 1989, Ozanne 1991, Pettersson *et al.* 1995, Walter and O'Dowd 1995, Esseen *et al.* 1996, Ozanne 1996, Hopkin 1998, Walter and Behan-
Pelletier 1999), with communities often large in *P. sitchensis* (Winchester 1997b). The Acarina and Collembola perform key habitat processes within the canopy such as nutrient cycling as well as being an important primary food source (Pettersson *et al.* 1995, Walter and O’Dowd 1995, Esseen *et al.* 1996, Hopkin 1998, Walter and Behan-Pelletier 1999), and their variation within canopies is often associated with changes in environmental conditions requiring moist and cool conditions provided by *P. sitchensis* (Lambert 1970, Hopkin 1997). The lack of significance in these trends for this study could be due to the plantations’ young age, limiting densities of the epiphyte community, an important factor for the above taxa, resulting in limitation of their populations.

Lichens are abundant in canopies, including in managed plantation systems (Rhoades 1995), although abundance is higher in old-growth conifer forests (Pettersson *et al.* 1995, Esseen *et al.* 1996). They have high fractal dimensions (Shorrocks *et al.* 1991) similar to woody plants, making them a complex habitat for small organisms, theoretically capable of supporting more 0.3 mm organisms than 3 mm species (Shorrocks *et al.* 1991). This should bias canopy communities towards small organisms such as Acarina and Collembola in areas of high epiphyte density and diversity. Different types of lichen also support various diversities and densities of invertebrates mainly as a result of their growth form, with macro-lichens supporting more invertebrates than crustose lichen communities (Stubbs 1989). Andre (1985) found Collembola associating with foliose and dis-cortical species, which have an open growth pattern, whilst Acarina associated with crustose species, those growing like a flat crust on the bark surface. Many correlations between lichen biomass and arthropod abundance have been reported in forest canopies.

Acarina are considered to contribute significantly to overall diversity of canopy communities, with evergreen tree species being especially mite rich (Walter and O'Dowd 1995, Walter and Behan-Pelletier 1999), studies reporting between 2 and 82% of arthropods collected being mites (Walter and Behan-Pelletier 1999). In the present research a mean of 14% and 33% of the arthropod community were Acarina, for *P. sylvestris* and *P. sitchensis* respectively, these results lay in the low end of the range, a response to the managed nature of the sites. Managed forests, due to their young age and disturbance events tend to have lower lichen diversities and densities, as the epiphyte communities are slow growing, requiring considerable periods in which to develop (Griffin and Conran 1994, Pettersson et al. 1995, Rhoades 1995, Esseen et al. 1996).

Although both collembolan and Acarina densities appear to be responding positively towards the canopy conditions of *P. sitchensis* (Table 5.1), probably a result of increased epiphyte density and microhabitat abundance, species richness of the two taxa show no differences between the two tree species (Table 5.2). These are surprising results as different tree species are expected to have very different species richness complements, with specific communities of invertebrates developing with specific lichen communities (Andre 1985, Walter and Behan-Pelletier 1999). However, the fact that the two tree species are conifers and under plantation conditions, could be restricting the richness of
the lichen community resulting in similar species richness between the two conifers. Research into the diversity of UK conifer lichen communities would be useful to establish whether differences between the two tree species lichen communities occur and how this might affect the micro-invertebrate community.

5.4.2 Species Richness and Species Lists.

As lichen communities are being held in an early successional state due to disturbance in the managed forests, the invertebrate community has low species richness due to restrictions in habitat diversity. Actual species richness levels for the two taxa were relatively low in the conifer species, with a mean of 3.5 and 3 Collembola species and 6.75 and 6.67 Acarina species in P. sitchensis and P. sylvestris respectively (Table 5.2). Acarina have shown diversity levels of up to 11 species on a single leaf in Australian rain forest (Walter and O'Dowd 1995) and 56 species of Oribatid mite in old growth P. sitchensis (Winchester 1997b), making the species richness level of approximately 6 to 7 species for the whole community here seem restricted. These greater diversities in the tropical and old growth habitats are expected, temperate plantation systems being less diverse, due to their young age and dense planting. Although previous research has concentrated on densities (Walter and Behan-Pelletier 1999) further research on the diversities of these organisms would be useful to see if values are closer to those of other studies. The low results here may be limited by the sampling technique, with some small organisms being lost due to air currents and the problems of taxonomic knowledge of the Acarina, little being known about their diversity levels and their lifestyles.
Despite the relatively low species richness of the two invertebrate communities, clear differences in the species present were seen. No species differences were seen between the two tree species, for Collembola, just four species being found on each (*Anurophorus laricis, Entomobrya nivalis, Lepidocyrtus curvicollis* and *Sminthurus fuscus*). However, some of these species are of interest, correspondence analysis of 100 collembolan species, with reference to microhabitat preference, highlighted *Entomobrya nivalis* as preferring trunks and rocks (Hopkin 1997), its presence in the canopies here is therefore unsurprising. All the species present are from genera that have a tendency to prefer the upper litter area of soils, the greatest percentages of their populations being found in this zone of coniferous forest soils in Wales (Hopkin 1997). This habitation of soil surface in turn makes them more likely to be species which travel vertically into the canopy (Hopkin 1997) when soil conditions become unfavourable due to either rain, which increases CO₂ concentrations in the soil (Bowden *et al.* 1976), or other factors. *Entomobrya nivalis* and *Anurophorus laricis* were also found to occur most abundantly over 1.2 metres above ground level in deciduous beech woodland (Lambert 1970). These collembolan species seem to be abundant in a range of tree species (Prinzing 1997), responding to the conditions provided by the canopy, rather than responding more directly to the tree species itself, being found on both conifer and deciduous species. The lack of variation in species present is therefore unsurprising, as the species are canopy specialists rather than tree species specialists.

Acarina species were different between the two tree species, with three unique species in each of *P. sitchensis* and *P. sylvestris* and six shared species (Table 5.3). This more
specific community within the tree species is associated with mite reliance on specific lichen species, which in turn respond very specifically to bark structure, as discussed above. The two tree species have very different bark types and environmental conditions, which will affect the lichen communities and therefore the Acarina species present. Many of these species especially in *P. sylvestris* are Oribatid, these are commonly over-represented in knockdown samples due to their relatively large size and a tendency to live in relatively exposed areas, they also dominate the acarofauna on bark (Walter and Behan-Pelletier 1999).

Relatively little is known of the Acarina species that inhabit UK coniferous plantation canopies due to their small size and taxonomic difficulty, although some information is available on the preference of some genera. The four most abundant species present in both tree species represent two each from the generally abundant and easily sampled Oribatida (*Camisia sp.* and *Chamobates sp.*) and the predatory order Prostigmata (*Anystis sp.* and *Bedella sp.*). Both the Oribatid species are capable of inhabiting quite diverse environmental conditions a number of species frequenting arboreal habitats (Wallwork 1976), with *Chamobates sp.* tending towards moss habitats. The Prostigmata species are known as outer bark predators having been found on a number of deciduous and coniferous tree species (Wallwork 1976), making them unspecialised predatory species.

The mite species unique to the tree species are more environmentally sensitive either at a regional scale (i.e. Yorkshire or Northumberland) or at a microhabitat scale. Specific information on the two groups of unique species is limited although a general pattern
seems clear. The three species unique to *P. sitchensis* (*Belba sp.*, *Pergamasus sp.*, *Platynothurus sp.*) have not been particularly recorded in the arboreal habitat, however they are all described as soil surface species (Wallwork 1970 and 1976). The *P. sitchensis* canopy must provide similar microclimate characteristics to the upper soil layers. Whereas the three *P. sylvestris* unique species (*Carabodes sp.*, *Cepheus sp.*, *Cymbaeremaeus sp.*) have been denoted as canopy species, *Carabodes* especially associated with the lichens on tree trunks (Wallwork 1976). The species are therefore more adapted to the more environmentally extreme conditions (higher temperature and lower humidity) found in the *P. sylvestris* canopy.

Just two significant results were recorded for mean invertebrate species richness between the two conifer species, with total invertebrate richness and coleopteran richness significantly higher in *P. sylvestris* (Table 5.2). Higher invertebrate richness in *P. sylvestris* (Figure 5.2) should be due to the species being native, the increased richness a result of the phytophagous aspect of the community being more diverse having adapted to the trees' chemistry. However, higher invertebrate richness seems mainly to be a result of higher species richness in the Coleoptera, few of which are phytophagous, and to a lesser extent the Araneae (Table 5.2). These species, particularly the Araneae are prey and habitat structure-specific which may be a more important environmental factor controlling the community in *P. sylvestris* than tree species *per se* and its chemistry.

The Trichoptera, Ephemeroptera and Mecoptera, all tourist species in the canopy habitat, occurred solely in *P. sylvestris*. Adult Trichoptera and Ephemeroptera do not feed, are
weak fliers remaining near water sources where their larvae develop, and use the open habitat of the *P. sylvestris* canopy for resting sites, whilst the Mecoptera could be feeding in the area, on dead animal and plant matter.

No significant results were seen in Araneae density and species richness between the two tree species, however *P. sylvestris* does seem to support more families and species of spiders than *P. sitchensis* (Table 5.4). *Picea sitchensis* supports spider species from three families whilst *P. sylvestris* has individuals from seven, four of which are unique (Araneidae, Clubionidae, Tetragnathidae, Thomisidae). The lack of significant difference between the tree species contradicts the findings of Ozanne (1991) - at least in the case of densities - who recorded significantly higher densities of spiders in *P. sitchensis*. A significant difference was seen in the mean species richness between the two tree species by Ozanne (1991 and 1996), *P. sylvestris* having a richer community, a similar pattern being found in the present data. *P. sylvestris* showed a trend towards higher Araneae richness compared to *P. sitchensis* with a mean species richness of 8 per m² ground area compared to 4.67 (Table 5.2).

The native status, large planting area and increased understory complexity could have accounted for the high species richness of Araneae in *P. sylvestris*. This would support the proposition that native tree species will have higher arthropod species richness than exotic introduced tree species having had time to develop complex communities (Southwood *et al.* 1982b, Kennedy and Southwood 1984, Claridge and Evans 1990). Of the four families unique to *P. sylvestris* two are of particular interest the Araneidae and
Tetragnathidae, both spinning orb-webs. Large spaces are required to construct orb webs so canopy structure and inter-needle/twig space needs to be great, making these species more common in pines, with their open structure (Greenstone 1984, Ozanne 1991). Their absence from *P. sitchensis* is a reflection of the denser canopy structure failing to provide suitable microhabitats for web construction. Seven species of Araneidae occurred in the *P. sylvestris* samples (Table 5.4) most of which are common and widespread (Roberts 1985), although a number of the species are worth further note. Four of the species are particularly associated with trees, *Cyclosa conica, Gibbaranea gibbosa, Nuctenea umbratica* and *Zygiella sp.*. *C. conica* is most associated with dark moist areas of woodland especially in evergreen areas and *N. umbratica* lives predominantly under bark. For the genus *Zygiella* just three species occur in the British Isles, one being found predominantly on pine trunks, however the invertebrate was not identified to species so it is unclear whether it is this pine specialist species. The Tetragnathidae specifically *Tetragnatha extensa* and *T. montana* found in *P. sylvestris* are widely distributed species, common throughout the British Isles. The two most common species of the genus in the UK are found in this data set, both of which prefer the habitat of grasses and low vegetation commonly close to water or boggy habitats, it is therefore interesting that these species should be found in the relatively dry habitat of the *P. sylvestris* canopy.

Thomisidae, another family found solely in *P. sylvestris*, are active hunters with many species having a preference for canopies (Roberts 1985), and occurring predominantly in southerly regions. Low prey diversity and the northerly situation of the *P. sitchensis* plantations could be limiting as a habitat for the Thomisidae. The only other family
unique to *P. sylvestris*, the Clubionidae, again prefers southerly regions of the UK (Roberts 1985), its failure to occur in *P. sitchensis* due to restrictions on range. The family prefers dry habitats with some species occurring predominantly on trees (Roberts 1985), its occurrence only in the *P. sylvestris* plantations is a response to the more open and dry habitat supplied, as well as their more southerly situation.

Three families occur in both tree species Linyphiidae, Metidae and Theridiidae. The last two show similar species complements in the two conifers and are generally widespread families common in a diversity of habitats (Roberts 1987), with Metidae spinning orb-webs and Theridiidae spinning complexes of criss-crossing webs. Linyphiidae, the sheet-web spinners, however show some important differences between the two conifer species, with high richness in *P. sitchensis*. Just four Linyphiidae species occur in *P. sylvestris* one of which is unique to the habitat (*Lepthyphantes tenuis*). Its presence solely in *P. sylvestris* is a result of regional distribution, being widespread in a number of habitats, but having a tendency to occur in more southerly regions (Roberts 1987). The three shared between the two tree species are widespread throughout the UK being common tree inhabitants, particularly *Drapetisca socialis* building its webs on the bark of trees (Roberts 1987). *Linyphia triangularis* is reported as being common in conifers (Parrack pers. comm.) and would be expected on both tree species. *Lepthyphantes expunctus*, despite being widespread on pines and other conifers, prefers southerly areas, records of its presence on *P. sitchensis* in Northumberland being scarce (Parrack pers. comm.).
Many of the other species occurring solely in the *P. sitchensis* samples are common but a few are worthy of further note. *Bolyphantes luteolus, Lepthyphantes alacris, L. zimmermanni, Pelecopsis nemoralis* the Metidae species and those in the Theridiidae family are all abundant and previously recorded in the *P. sitchensis* plantations of Kielder (Parrack pers. comm.). However *L. obscurus* although previously recorded is uncommon in the habitat, due to its general rarity in this country whilst *Pityohyphantes phrygianus* is reported as a newcomer to Northumberland with just one or two records (Parrack pers. comm.). The latter species is the only one of the genus occurring in Britain where it is considered a recent colonist restricted to conifer plantations in northern England and Scotland (Roberts 1987) having extended its range down from Scotland into the plantations of Northumberland. It appears that there is a bias in the *P. sitchensis* Araneae community towards the Linyphiidae, the canopy structure suiting the construction of sheet-webs (Gunnarsson 1988). Whilst in *P. sylvestris* Araneae are more diverse across the families and many different lifestyles, filling the many habitats provided by the canopy and its understory.

The Coleoptera contributed significantly to the species richness of *P. sylvestris*, with three times the number of species compared to *P. sitchensis* (Table 5.2). This is in contrast to the findings of Ozanne (1991), who reported no significant difference in mean species richness between the canopy communities of Coleoptera in *P. sylvestris* and *P. sitchensis*, but high abundances of Coleoptera in *P. sitchensis*, not found in the present data. *Pinus sylvestris* had seven families not found in *P. sitchensis* (Table 5.5), most occurring in low densities (Figure 5.4), and five species of Coccinellidae not found in *P.
The two species shared seven families some of which showed low densities in both tree species (Cryptophagidae, Curculionidae and Lathridiidae) two showing high densities (Coccinellidae and Staphylinidae) and Carabidae and Chrysomelidae having higher densities in *P. sylvestris*. The different lifestyle preferences of these beetle families mean they were responding to different aspects of the two tree species, either food supplies or habitat, resulting in the differences seen in the species/families present.

The seven families shared by both tree species are ubiquitous beetles with a range of species adapted to many habitats and lifestyles, however some showed higher densities in one or other of the tree species, responding to the specific conditions provided. The Carabidae showed higher densities in *P. sylvestris* (Figure 5.4), these are predominantly ground species but travel into the understory and main canopy to hunt. Higher densities and diversities have been reported for ground Carabid in small forest fragments compared to large, thought to be a response to higher vegetation diversity in these sites (Halme and Niemela 1993). This response to vegetation diversity could also be present in the canopy Carabid community in *P. sylvestris*, where higher mean densities result from the more complex understory encouraging vertical movement of the beetles into the canopy. The response could also be due to prey availability because, although general arthropod abundance is a little lower in *P. sylvestris* compared to *P. sitchensis*, a more diverse and generally larger (size) invertebrate prey community is more abundant in *P. sylvestris*.

Chrysomelidae, the leaf beetles, also showed higher densities in *P. sylvestris*. These beetles are host-specific feeding on living plant tissue. Their increased densities in *P.
*sylvestris* is either a response to increased adaptation to the plant chemistry or a response to the complexity of the understory, with more plentiful and different vegetation in the area generally encouraging more herbivorous organisms and in general, many more phytophagous Coleoptera recorded in *Pinus* compared to *Picea* (Winter 1983).

The Curculionidae were found in low densities on both tree species, these are the plant feeding weevils which are likely to be different species on respective conifers adapted to feed on the specific chemistry of each. Their general low abundance is expected, small populations being the norm until outbreak conditions apply when they can be serious pests (Speight and Wainhouse 1989, Day and Leather 1997, Speight *et al.* 1999). The Cryptophagidae and Lathridiidae also found on both tree species are general scavengers of decaying material. Staphylinidae were the final family of beetles to be found in both tree species, again these are a ubiquitous predatory family found in many habitats, their slightly higher density in *P. sitchensis* could be a response to slightly higher densities of prey items.

Seven families were found solely in *P. sylvestris*, a number of these were predatory species (Cantharidae, Cleridae, Melandryidae), the others being plant feeders or scavengers (Elateridae, Nitidulidae, Salpingidae, Scolytidae). The increased numbers of predatory beetle families could be a response to a more diverse invertebrate community in *P. sylvestris* and therefore more specialist prey items. Indeed many of the Cleridae and Melandryidae species are specialist bark beetle predators (Chinery 1993) preying on the Scolytidae which were solely captured in *P. sylvestris*. Scolytidae are more likely to have
adapted to the chemistry of *P. sylvestris* due to the increased time in the flora, ensuring a community of this family and its specialist predators has developed on the native tree species, many more bark beetles being reported in *Pinus* compared to *Picea* (Winter 1983). Cantharidae are predators of flower-visiting invertebrates often preferring to hunt on the Umbelliferae, again the presence of a diverse understory including flowering species would increase the likelihood of this family being found in the habitat. In a similar way the Elateridae are pollen, nectar and plant feeders which are likely to be present due to the high understory complexity not found under *P. sitchensis*.

The Coccinellidae which occurred in both tree species were further classified to species, some interesting differences were seen between the two conifer species. The family included the most abundant beetles in both tree species (Figure 5.4), with seven species in *P. sylvestris* and three species in *P. sitchensis*, one of which was unique to *P. sitchensis* (Table 5.5). The Coccinellidae are predatory beetles with sucking rather than biting mouth-parts often associated with aphid communities. Although they are predatory species they sometimes associate with specific plant communities such as heather or conifers, either a reflection of an association with specific microhabitat conditions or a response to specific prey items being on specific plant communities. Most of the species found in the two conifers are widespread throughout many habitats, however two are of note *Anatis ocellata* and *Aphidecta obliterata*, which are both associated with coniferous trees. *Aphidecta obliterata* is the only species unique to *P. sitchensis* being specially adapted to the conditions provided by this recently introduced species.
Mean densities of guilds differed between the two tree species, *P. sitchensis* having more detritivores, herbivores, predators and scavengers per m² ground area than *P. sylvestris* with just the tourists having higher densities in *P. sylvestris*. The high densities in *P. sitchensis* were caused by the combination of a number of taxa with high (although not significantly) densities compared to *P. sylvestris*. The particularly high densities of some Acarina species, e.g. Collembola and Psocoptera in *P. sitchensis*, all responding to the cool, moist conditions and high dead organic matter, resulted in the high densities of detritivores. The herbivores were particularly biased by the Hemiptera densities again higher in *P. sitchensis* (Table 5.1) and the scavengers by the number of different scavenging beetles. One of the strongest responses was seen in the predatory guild (Table 5.6) a combination of the particularly high densities of the predatory Acarina, Araneae and Coccinellidae beetles causing the higher densities of predators per m² ground area in *P. sitchensis*. High phytophagous and predatory guild densities and percentage contributions have been reported in old growth *Picea sitchensis* the high predator loading maintained by the structurally and functionally diverse ecosystem (Winchester and Ring 1996, Winchester 1997a and b). However similarly high levels in the plantation system would not be expected with the system failing to have reached a climax community, the results here show the same emphasis towards community dominance by the herbivores and predators the pattern being established early in the canopies’ life. The establishment of a consistent community from a young age supports the findings for the Heteroptera in
pines which were found to establish distinct communities early in the trees' life and being maintained throughout its life (Cmoluchowa and Lechowski 1993).

The high predator numbers were reflected in the predator/prey ratio analysis, *P. sitchensis* having a significantly higher mean predator/prey ratio than *P. sylvestris*, the species having higher numbers of predators to prey within the canopy. *Picea sitchensis* has an invertebrate community, at least some aspects of which are under considerable predator pressure. These high predator levels are a result of a few species of predators utilising a relatively simple prey community biased towards the herbivores and detritivores. Research on larch and beech trees has found the dominant predatory species (Araneae) taking unequal quantities of three epiphyte herbivore orders (Psocoptera, Homoptera and Collembola), the spiders actively selecting the 'large but rare' Psocoptera over the 'common and small' Collembola (Turner 1984). It is likely that similar energetic decisions are being made in the conifer canopies with predator pressure being higher on the larger Psocoptera and Homoptera than the small Collembola, accounting for the high populations of the Collembola seen in the canopy.

As seen in other results the tourist aspect of the invertebrate community is considerably denser in *P. sylvestris* backed up by the guild analysis, the tourists also contributing a greater percentage to the community of *P. sylvestris*. As discussed the more open habitat and the complex understory along with the native status of the tree species encourages transient tourist invertebrate species to occur in the canopy, either using the area as a resting site, or, more usually, inhabiting the understory beneath as a site for reproduction.
Similar findings have been noted for deciduous tree species within Britain with a higher percentage of the community being tourists in the native species (Betula and Quercus) compared to the introduced Robinia (Moran and Southwood 1982).

As well as the differences in guild structure between the two tree species, intra-order guild structure (for the Acarina and Coleoptera) showed some variation between the tree species. The Acarina predators and detritivores both showed higher densities in P. sitchensis, a result biased by the generally higher (although not significantly) densities of Acarina in P. sitchensis as a whole. Some response in the Acarina guilds is however occurring as the predatory mites also constitute a greater percentage of the community and show greater species richness in P. sitchensis compared to P. sylvestris. High species richness of these organisms will be a response to the diverse lichen communities within the cool and moist P. sitchensis canopy and the high densities of small prey items (other Acarina and Collembola) in the canopy. These increased diversities and densities of predatory mites also contributed to the higher predator/prey ratios in P. sitchensis.

The guild structure within the Coleoptera varied between the tree species with P. sitchensis having a simplified community compared to P. sylvestris dominated by the predatory guild again contributing to the high predator/prey ratio. The simplified guild make up of the Coleoptera is due to the lack of diversity at a larger scale within the habitat compared to the diverse Acarina guild, a result of the small scale structural complexity of the canopy. The Coleoptera also have a particularly limited phytophagous community compared to P. sylvestris due to the limited time P. sitchensis has been in the
UK flora, the beetles having yet to develop mechanisms for dealing with the trees’ chemistry. *Pinus sylvestris* meanwhile shows a more even coleopteran community with similar densities of the various guilds and a more species rich herbivore community compared to *P. sitchensis*. More herbivorous species are capable of feeding on *P. sylvestris* due to its increased time in the flora and the more diverse understory beneath it. In addition some of the species use the canopy of *P. sylvestris* as a resting site. This more balanced community structure is a reflection of the more climax community expected on a native species which has little movement of species onto it unlike an introduced species which is still gaining its invertebrate complement.

Many responses seen in the invertebrate communities between the two tree species are following the expected trends due to the differences between the tree species’ time in the flora, chemistry, structure and regional positioning. The invertebrate community in *Pinus sylvestris*, particularly the herbivorous aspect of the community, would be expected to be more species rich, have less detritivores due to the warmer and more open canopy affecting canopy epiphyte abundance and have more tourist species. In all cases these trends are held true, the invertebrate community as a whole was more species rich in *P. sylvestris* along with the Araneae and Coleoptera, with many more species and tourist species inhabiting the many niches available in the canopy. The increased Coleopteran richness is particularly interesting following similar results where coleopteran richness was increased in more open canopy habitats (Greatorex-Davies *et al.* 1994). Although densities of herbivores are higher in *P. sitchensis* the richness is again higher in *P. sylvestris* particularly for the Coleoptera herbivores, due to the invertebrates having
adapted to the trees’ plant chemistry during its long presence in the UK flora. These patterns of increased richness of tourist and herbivore species are associated with a reduced richness and density in the detritivore and scavenging aspect of the community.

Fewer detritivores would be expected in the *P. sylvestris* canopy due to the open conditions there leading to a less diverse and abundant epiphyte community, the pattern being reversed in the case of *P. sitchensis* with its dense cool and moist canopy and high standing dead organic matter encouraging large epiphyte communities. The small and microclimate-dependent invertebrates showed clear responses to the *P. sitchensis* canopy, many more Acarina and Collembola being associated with the habitat. Of particular interest is the fact that more fungivore Acarina species are particularly associated with the *P. sitchensis* canopy, inhabiting the epiphyte community, whereas the two tree species share the predatory species of Acarina which are less specific about their habitat/prey requirements.

Along with these responses, species lists varied considerably between the two tree species with a number being specific to one or other of the tree species either due to the chemistry or structure of the tree or its regional positioning and therefore the climatic conditions it provided. A number of Araneae particularly responded in this manner, some species being structurally specific about their habitat and the ability to construct webs, others having southerly distributions and not occurring in *P. sitchensis* due to its northerly distribution. Interestingly a pattern opposite to that expected following previous research was found in the Araneae. Thomisidae and Theridiidae should inhabit canopies
with high needle densities (P. sitchensis) suitable for scaffold-webs whilst Linyphiidae should prefer more open areas (P. sylvestris) in which to construct sheet-webs (Gunnarsson 1988, Ozanne 1991). However the present study found an opposite trend with more species of Theridiidae and Thomisidae occurring in P. sylvestris and more Linyphiidae species in P. sitchensis. It appears that regional distribution is having more of an effect on the presence of these families than the structural dimensions of the respective canopies, with the Thomisidae and some of the Linyphiidae having southerly distributions limiting them to the P. sylvestris canopies, even though if the two species were occurring in the same region they might preferentially build their webs in P. sitchensis.

Clear differences are seen in the canopy invertebrate community between the two conifer species, apparent at the density, richness, species and percentage contribution levels. In many cases the patterns are supporting previous research, with higher general densities in P. sitchensis, particularly with the small detritivore community, and higher richness in P. sylvestris. These patterns appear to show a strong response of the invertebrates to the native condition, structural complexity and floral diversity of the two habitats. Picea sitchensis is an introduced species and therefore supports fewer species than P. sylvestris, however its planting should not necessarily be discouraged, as it appears to be not just important, but increasingly important, for a number of invertebrate species. This is especially true for some of the Araneae species, which in turn are considered an important winter food supply for passerine birds (Pettersson et al. 1995). The results also highlight the importance of P. sylvestris plantations as they support a diverse and natively
important invertebrate community which would otherwise be limited to the few remaining areas of natural Caledonian forest if *P. sylvestris* was not used as a plantation species.
CHAPTER 6. DISCUSSION.

The present research aimed to increase the information available on the invertebrate communities present in the canopies of conifers under plantation conditions and specifically how these communities are affected by the proximity of plantation edge, tree species and the implementation of plantation management. Invertebrate communities are an important aspect of the forest system performing many ecological functions, including nutrient cycling and acting as a primary food source for both birds and mammals (Jansson and von Bromssen 1981, Schowalter et al. 1981, Hansson 1983, Pettersson et al. 1995, Lowman 1997, Speight et al. 1999). Unique and complex invertebrate communities are found within all areas of forests including the soil, leaf-litter, understory and canopy layer (Erwin 1982, Day and Carthy 1988, Stork 1988, Allison et al. 1993, Hollier and Belshaw 1993, Simandl 1993, Hammond et al. 1997).

Due to this diversity and uniqueness of the canopy flora and fauna and the improvement of access techniques to the canopy system, research into the habitat has increased in recent years, highlighted by the rate at which publications based on canopy research are outstripping that of general biological publications (Nadkarni and Parker 1994). The use of chemical knockdown techniques particularly allow a broad cross section of the invertebrate community from the canopy to be sampled allowing detailed community research to be performed.
Much canopy research has concentrated on the tropical forest system due to its high diversity and endemism but also the high level of anthropogenic pressure. Studies have particularly concentrated on the plant, epiphyte and bird communities of these habitats, because of the relative ease with which these species can be studied and the bias in scientific expertise towards them (Blake and Karr 1984, Lovejoy et al. 1986, Lowman and Nadkarni 1995). Also studies of single species or orders rather than communities are widespread due to the complexity of trying to ascertain community associations. Research into temperate forest canopies in general is less common (Ozanne 1997) although canopy invertebrate community research in temperate areas has been on the increase in recent years with a number of key studies (Schowalter et al. 1981, Southwood et al. 1982a, Majer and Recher 1988, Schowalter et al. 1988, Pettersson et al. 1995, Schowalter 1995, Niemela 1997, Ozanne et al. 1997, Winchester 1997 a and b). However specific invertebrate research in United Kingdom conifer canopies is particularly lacking with just a single study concentrating on the whole invertebrate community of conifer canopies (Ozanne 1991).

The lack of research into conifer canopy invertebrates in the UK is an important issue as these forests, particularly those of introduced species, have become widespread in recent years dominating the UK flora. This has resulted in a dramatic shift in the type of forest habitat available to invertebrate species in recent history. Research is required to assess the use invertebrates make of this new habitat and how they are reacting to the specific conditions of plantation forests, i.e. are these exotic forests capable of supporting complex invertebrate communities and nationally important forest specialist species?
One of the key differences between plantations and natural forests is the system of roads and tracks running through plantations resulting in large quantities of edge habitat and increased edge-effect pressures. Analysis of the depth of these edge-effects in various forest types have shown that they are predominantly associated with the first 50 metres of the forest habitat although effects have been reported for many hundreds of metres (Williams-Linera 1990, Laurance 1991, Chen et al. 1992, Young and Mitchell 1994, Chen et al. 1995). Conifer plantations, due to their system of tracks and roads, are going to be particularly susceptible to edge-effects, which could severely affect the invertebrate communities inhabiting the area.

Research into edge-effects in invertebrates of UK conifer canopies has previously concentrated on the first 50 metres of *Pinus sylvestris* and *Picea abies* plantations (Ozanne 1991, Ozanne et al. 1997), however this research would have failed to establish any edge-effects occurring in the invertebrate community beyond this depth. The concentration on these tree species although both important, *P. sylvestris* being the only native conifer species used in plantation conditions, also neglects to investigate the most widely planted conifer species in the UK. Since its introduction in 1831 *Picea sitchensis* has become the most commercially important tree in the UK, it is vital that the effect of edge proximity on the invertebrate communities within this tree species is known. The present research extended the analysis of edge-effects to a greater depth (100 metres) in two species of conifers in the UK (*P. sylvestris* and *P. sitchensis*) to establish the edge-effect depths for the complete canopy invertebrate community beyond 50 metres and to
establish whether edge-effects differ between tree species planted under similar conditions.

The occurrence of edge-effects within forest systems results in a proportion of every forest patch being under the influence of edge proximity with the remaining patch area maintaining the normal forest conditions - or core conditions - preferred by forest specialist invertebrates. Models have been developed which calculate the proportion of these edge and core habitats within patches of different areas and shapes (Laurance and Yensen 1991, Malcolm 1994). These provide a more accurate reflection of the quantity of habitat within any fragment capable of supporting either edge or core communities, with the proportion of core area found to be a more accurate reflection of bird abundance than total patch area (Temple 1986). As well as assessing the proportions of edge and core habitat available to organisms the models can be further manipulated to assess the effects of management activity on the relative proportions of the two habitat types.

Increased diversity in habitat edges has often been used as a conservation argument to encourage the maximisation of edge habitat within forest systems (Helle and Muona 1985, Greatorex-Davies 1991, Baldi and Kisbenedek 1994, Bedford and Usher 1994). Specific management including the removal of areas of trees along forest perimeters has been suggested to increase the convolution of forest edges and therefore the relative proportion of edge habitat (Greatorex-Davies 1991), indeed this has been shown to be beneficial for some species including the Lepidoptera (Greatorex-Davies 1991). However increased diversity at forest edges is only seen for some species, often generalists
(Peltonen et al. 1997), the effect of management on sensitive core species and forest specialists has not been assessed. Using the information gathered on invertebrate community responses to edge proximity in this study and various species’ preferences for either edge or core habitat the proportions of the two types of habitat were calculated for the research patches. Further manipulation of the research patch shape allowed the calculation of the changes in the proportions of edge and core habitat after the implementation of edge management and therefore the likely knock-on effects for invertebrate communities.

Further to this issue of edge proximity and proportions of edge and core habitat within a habitat patch is the differences in invertebrate communities as a result of the tree species they occupy. Variations in invertebrate communities living on different species of plants have been reported in many studies (Southwood et al. 1982 a and b, Strong et al. 1984, Basset et al. 1996) a result of the plants’ chemistry, structure, length of time in the flora, land area covered and regional climate, all affecting an invertebrate’s capacity to associate with a plant. Floral species with complex chemistry and low structural complexity, which have covered a small area for a short period of time, are likely to have a less diverse invertebrate community than a species with less complex chemistry, high structural complexity and a wide and abundant distribution within the landscape (Claridge and Wilson 1976, Lawton 1983, Claridge and Evans 1990, Denno and Roderick 1991). A plant’s chemistry has a particular effect on herbivorous species which either require a long time to adjust to the plant’s chemistry or for it to be relatively simple before large communities can develop. Structural complexity is related to the quantity of
microhabitats available within the habitat and therefore the diversity of invertebrates capable of inhabiting them, a structurally complex plant has many microhabitats which can support a complex community of specialised invertebrates (Claridge and Wilson 1976, Denno and Roderick 1991). The abundance of a plant in the landscape will also affect its invertebrate community, a widespread plant will not only provide more habitat for the invertebrate but will also be more apparent within the landscape encouraging mobile species to settle in the area.

Data appropriate to answer the three main research questions were collected using replicate transects running perpendicular to plantation edge into patches of each of the two tree species (Chapter 2), with chemical knockdown samples taken at 5, 10 and 20 metre intervals from the edge to a depth of at least 100 metres. The knockdown technique ensured that a representative cross section of the invertebrate community was collected allowing analysis of the data with reference to order species, richness, diversity and guild variation. Research comparing the efficacy of techniques for collecting invertebrates from the canopy has shown that chemical knockdown provides the highest number of a representative cross section of the community compared to other techniques such as branch clipping or beating. Chemical knockdown samples more species than other methods (Majer and Recher 1988) and compares well to faunal lists for any given community (Southwood et al. 1982b).

Many invertebrates were shown to respond to edge proximity either positively or negatively in the present research with some responding to a depth greater than 50
metres, a pattern missed by previous research on edge-effects in *P. sylvestris* and *Picea abies* (Ozanne 1991, Ozanne *et al.* 1997). Ozanne (1991) established no variations in invertebrate species richness due to proximity of plantation edge, however abundances of orders did vary between the edge and core habitats. Epiphyte feeders including the Collembola and Psocoptera and carnivores including Araneae and Hymenoptera showed increased abundance in the core area while herbivores of the Homoptera and Acarina showed increased abundance in the edge zone (Ozanne 1991). These patterns are thought to be a response to the increased quantity of epiphyte growth in the core area, due to higher humidity levels and the increased foliage at the edge of forest plantations due to lateral branch growth.

In the present research responses to edge proximity were seen for species richness, diversity and invertebrate abundances in both tree species. For *P. sylvestris* invertebrate communities no positive responses to edge proximity were found, with densities and species richness both significantly higher in the core habitat 80 to 100 metres from plantation edge. Epiphytic feeding Collembola showed considerably higher densities per metre squared ground area in the core, a response to the moister conditions and high epiphyte communities in this area (Esseen *et al.* 1996), supporting the findings of Ozanne (1991). A similar pattern was seen in *P. sitchensis* with the Collembola and specifically *Entomobrya nivalis* showing high abundances in the core habitat, the only invertebrate to respond positively to the core habitat of *P. sitchensis*. Collembola are particularly environmentally sensitive species (Lambert 1970, Hopkin 1997) and require specific epiphytes as food sources which themselves respond to key environmental conditions.
(Stubbs 1989, Pettersson et al. 1995). In a similar way the Acarina in general, and *Chamobates sp.*, *Cymbaeremaeus sp.* and *Anystis sp.* specifically, show increased densities in the core of *P. sylvestris* along with increased species richness within the area, dependent on the microclimatic conditions and the available food sources. The first two are detritivore/fungivore species responding to the habitat in a similar way to the Collembola. *Anystis sp.* is also responding to food availability in the core habitat being a predatory species thriving on the higher densities of small invertebrate prey in the core area.

Both the Collembola and Acarina have been reported as being important in the nutrient-cycling and formation of canopy soils in forests (Winchester and Ring 1996), their presence is therefore likely to be vital to the health of the canopy system and should be encouraged. To ensure abundant and diverse communities of these primary consumers within the conifer canopy, areas of core habitat in both tree species should be maintained.

Two species of Araneae showed increased densities in the core area of *P. sylvestris*, *Drapetisca socialis* and *Leptyphantes expunctus* these are specialist forest species responding to the core habitat of this native tree. The species are particularly responsive to the bark structure of the trees they inhabit, building their webs amongst the bark ridges (Roberts 1987), although this cannot solely account for their preference for core habitat as bark structure should be similar in both edge and core areas. Abiotic conditions and the availability of large quantities of prey items within the core area of *P. sylvestris*, reflected in the high diversity and abundance of invertebrate species in the core, must also account
for the presence of these predatory forest specialists. Increased densities and species richness of Araneae have previously been reported in *P. sylvestris* (Ozanne 1991, Ozanne *et al.* 1997) supporting the pattern found in the present research.

Overall the invertebrate community in the core habitat of *P. sylvestris* is more diverse than the edge, supporting a large number of invertebrate species including a number of tourist species, epiphytic communities (Collembola and Acarina) and structurally dependent predatory forest specialist species (*Drapetisca socialis*, *Leptypyantes expunctus*). These results highlight the importance of core habitat in *P. sylvestris*, which should be encouraged if a healthy forest system supporting a number of rare forest species is to be encouraged. The full depth of effects of edge proximity were not highlighted by the previous research in *P. sylvestris* (Ozanne 1991) which clarifies the need for at least 100 metre transects to investigate edge-effects in *P. sylvestris* conifer canopies.

One pattern reported by Ozanne (1991) but not seen in the present research was a high abundance of herbivorous species in the edge habitat, this was associated with increased plant material at the edge due to lateral branch growth. Although the *P. sylvestris* trees used in the two samples were of a similar age and height, extensive lateral growth was not seen in the trees of the present research, due to specific management strategies, resulting in the lack of an increase in herbivores at the edge. It therefore appears that some but not all edge-effect patterns in the invertebrate communities of *P. sylvestris* are consistent across plantations and years. Relatively stable responses are seen in the
Collembola and Acarina to core habitat across both studies reflecting a constant response of the small and often ignored yet important detritivore community to the core habitat of *P. sylvestris*. Edge-effects seen in the herbivores are a particular response to variations in the growth of the trees which can be highly variable between sites and years but they are less likely to be useful as a tool for comparing canopies. Therefore Collembola may prove to be more of a conservation tool than other more apparent species used, unless specific conservation of these species is required, such as the Coleoptera and Lepidoptera whose responses tend to be more variable between plantations and show the predominance of responses to edge habitat.

*Picea sitchensis* showed different edge-effect responses in the invertebrate community highlighting the need to research plantations of different species independently, it cannot be assumed that the edge-effects seen in the community of one species will be the same as those in another. No previous research has been carried out in the UK on the invertebrate community of the canopy of *P. sitchensis* with particular references to edge-effects and only limited work has been performed on edge-effects in *P. sitchensis* in other countries. Edge-effects in the ground invertebrate fauna of mixed spruce and pine forests in Finland reported a preference for the edge habitat in six invertebrate groups (Helle and Muona 1985), a similar pattern to that of the canopy community in the UK. The predominance of responses were seen in the edge of the *P. sitchensis* plantations with increased densities, species richness and diversities of all the invertebrates but particularly the Araneae, Acarina, Coleoptera and Diptera.
The Coleoptera, important predators of pest species such as *Elatobium sp.*, especially *Aphidecta obliterata* (Coccinellidae) a conifer specialist, showed the most consistent responses to edge proximity in *P. sitchensis* with both higher densities and species richness in the edge habitat. This is a direct response to increased abundance of the Hemiptera in the edge, which are feeding on the increased lateral growth seen in the edges of *P. sitchensis* plantations. Ground Coleoptera have also been shown to respond to the shading of forest habitat with open less shaded areas (edges) encouraging high densities and species richness (Greatorex-Davies *et al.* 1994). Diptera showed increased abundance in the edge habitat. The order often shows clumped distributions in canopies (Didham 1997) associating with open areas within the canopy which allow ease of flight (Didham 1997), their presence in the edge is therefore following predictable patterns in distribution. Species richness and diversity in the Diptera are also affected by edge habitat, being higher in the structurally complex edge habitat (Didham 1997). No variation in species richness was seen in the present research as Diptera were not identified to species, however from visual assessment of the samples edge and core communities appeared similar, so the present data do not support the findings of Didham (1997).

Unlike the findings in *P. sylvestris* the Araneae failed to respond to core habitat in *P. sitchensis* being found in higher densities in the edge habitat, particularly the Linyphiidae. The bulk of Linyphiidae were of the genus *Leptphyantes* considered a woodland specialist genus which would be expected to be found in typical forest habitat, namely the core. It appears here that the edge of *P. sitchensis* plantations are actually
providing the ideal woodland habitat for invertebrate species, the core habitat being too
dark and moist with low quantities of living plant material for herbivores to utilise.
However, as mentioned, the core habitat does support high densities of Collembo
utilising the high epiphyte abundance in the core conditions.

As well as these specific responses by orders to edge habitat, overall invertebrate species
richness and diversity were significantly higher in the edge habitat of *P. sitchensis* in
contrast to the pattern in *P. sylvestris* seen in the present research and that of Ozanne
(1991). An opposite result for the same genus of tree was recorded by Ozanne and
colleagues (1997) they found overall higher densities and richness in the core area of
*Picea abies*. The invertebrate communities of the two tree species are responding in very
different ways to edge proximity with a diverse community of forest specialist species
occurring in the core habitat of *P. sylvestris* and a relatively simple community of
invertebrates in the edge habitat of *P. sitchensis*, with an abundant Collembo
community in its core habitat. For *P. sylvestris*, core habitat is the area of highest
invertebrate diversity and should be encouraged whereas maintaining edge habitat is key
to maximising invertebrate species diversity in *P. sitchensis*.

As well as the community response being different between the two trees, individual
orders respond to edge proximity in very different ways, suggesting different
invertebrates should be used as indicator species in the two conifers. Indicator species are
a common tool in conservation biology (Spellerberg 1992), a single species, often rare,
being used to assess the quality of a habitat or the response of an area to management, if
the species is present and unaffected by the management the habitat is considered to be healthy. Coleoptera have been especially researched with reference to edge proximity in both the temperate and tropical regions (Helle and Muona 1985, Day et al. 1993, Bedford and Usher 1994, Greatorex-Davies et al. 1994, Ozanne et al. 1997), this is partially due to a bias in taxonomic knowledge towards the Coleoptera and their size and visibility within a habitat. The responses of beetles to edge proximity have sometimes been used as a reflection of the total invertebrate community response to the edge. This may be an appropriate assumption in *P. sitchensis* plantations where coleopteran richness and density is higher in the edge habitat where the bulk of invertebrate richness is found, however they would be a poor indicator tool in *P. sylvestris* where they fail to show significant responses to edge proximity. For the native *P. sylvestris* plantations it would be more appropriate to use the less high profile but still important invertebrates such as Collembola and Acarina which show consistent responses to edge proximity, unless the maintenance of Coleoptera numbers was the conservation aim. For habitats where edge-effect responses are not known the use of a fleet of indicator species (Collembola, Araneae and Coleoptera) representing a number of feeding guilds and abiotic requirements may be the way to analyse habitat quality - a more community based analysis technique rather than the use of single species.

Further to the establishment of how different invertebrates responded to edge proximity, Chapter 3 aimed to define the actual depths of edge-effects for different organisms, which could be used in the core-area model (Chapter 4). A technique recently applied to ecological data for establishing the position of edge-effects is squared euclidean distances
which calculate the difference between adjacent sample points looking for points of high contrast between samples, highlighting different adjacent communities (Brunt and Conley 1990, Johnston et al. 1992). The technique has proved useful at the landscape level (Johnston et al. 1992), however the technique was of limited use with the present data placing the edge-effect depth almost always at 5 metres. Although high contrast did occur between the zero and 5 metre samples this fails to reflect the more subtle edge-effects occurring to greater depths in the plantations.

Visual estimation appears to reflect a more accurate edge-effect depth than the SED technique, placing edge-effect depths at various distances from 5, 30 and 80 metres depending on invertebrate species. Those species showing positive responses to edge proximity appeared to prefer the first 5 to 30 metres of plantation edge, which are the depths associated with the most rapid changes in abiotic conditions. In *P. sylvestris*, where invertebrates were responding to core habitat a number of the responses were not apparent until 80 metres plus from plantation edge. This highlights the necessity for transects running to a considerable depth into plantation patches to ensure that edge-effect responses are not missed. If visual assessment is to be relied on to establish the depth of edge-effects, it must be ensured that replicate transects have been performed allowing the analysis of graphs with clear mean data.

The variation in the depth of edge-effects seen in the invertebrate communities has an obvious effect on the proportion of edge and core habitat available to different species in any given patch size, not all the patch being suitable for habitation. Calculation of the
quantities of edge and core habitat in conifer patches was the aim of Chapter 4 using the core-area model (Laurance and Yensen 1991), enabling the assessment of a patch's ability to support minimum viable populations and the effects of edge management on the proportions of edge and core habitat. Many studies have centred on total patch area to assess its capacity to support diverse communities (Diamond 1975, Harrison et al. 1988, Shrader-Frechette and McCoy 1993, Andren 1994), the species area relationship suggesting that increased patch area results in higher species richness (Simberloff 1976, Connor and McCoy 1979, Claridge and Evans 1990). However since the establishment of the effects of edge proximity on forest habitats, total patch area has been found to be a poor predictor of species diversity within a patch compared to that of core area (Temple 1986). It is therefore the case that depending on the habitat preference of a species either for edge or core habitat, patches of different sizes and proportions of these habitats should be encouraged rather than just a certain sized patch overall.

The development of core-area models (Laurance and Yensen 1991, Malcolm 1994) allows the calculation of the two quantities of habitat by a simple equation using patch area, perimeter length, edge-effect depth and patch shape index (Patton 1975). The model has been applied to a number of sets of hypothetical and field data where it has proven to be a more accurate predictor of likely species diversity within a patch. The model's developers, Laurance and Yensen (1991) proposed a minimum percentage core area value that should be maintained in a patch to support a highly diverse community, some 50% minimum core habitat. This figure proved useful with the data they used with core habitat being vital to species occupation of the habitat, however this 50% minimum core
area may not be the best possible guide line for proportions of habitat in all circumstances. In cases where edge habitat provides the bulk of the diversity of the overall community, such as the *P. sitchensis* plantations above, the quantity of core habitat is somewhat irrelevant and edge habitat needs to be encouraged to maximise invertebrate diversity. A further issue with the 50% minimum core area suggestion is the actual size of the patch. In patches that are quite small, each may be supporting either 50% edge or core habitat depending on the desired area but these may only constitute a few hectares of habitat. In this case it may be considered that the patch is adequately supporting specialist species as it has 50% of the desired habitat when in actual fact the area is below that capable of supporting minimum viable populations (Muhlenberg *et al.* 1991).

In Chapter 4 edge-effect depths of 5, 30 and 80 metres were applied to the research patches in *P. sylvestris* and *P. sitchensis* using the core-area model (Laurance and Yensen 1991), assessing the quantities of edge and core habitat in the two tree species with their different average patch sizes. The relatively large *P. sitchensis* patches were found to be heavily biased towards core habitat even with the 80 metre edge-effect depth. The patches were therefore favouring the core habitat with its low species diversity representing a community dominated by Collembola and Acarina. *Picea sitchensis* patches of this size (approx. 60 hectares) in the UK are failing to maximise their invertebrate diversity having thin strips of habitat with high invertebrate diversity. By encouraging edge a diverse invertebrate community could be maintained within the tree species adding to the overall diversity of the regional landscape. The quantity of edge
habitat could be maximised in the landscape by a number of means, reducing patch area
would naturally result in a greater proportion of edge habitat within the landscape as
would an increase in convolution of the perimeters (see below).

Hypothetical application of edge management techniques, resulting in increased
convolution of the edges, were applied to the research patches by re-analysing the
changes in patch area and perimeter length resulting from the cutting of box junctions and
bays in the patches. These two methods of edge management have been proposed as
suitable techniques to increase the quantity of edge habitat in forest systems particularly
to encourage lepidopteran species (Greatorex-Davies 1991). Box junctions involve the
cutting back of trees at the intersections of forest tracks, whilst bays are coves of trees
removed along the length of patch edges. Both techniques to a greater or lesser degree
result in a loss of patch area and an increase in the convolution of the patch edge which
should result in higher shape indices and therefore more edge habitat in a patch of any
given size.

An unexpected negative effect was seen when box junctions of 10 and 20 metres were
applied to the P. sitchensis patches with the quantity of edge habitat reduced rather than
increased, a result of the small change in perimeter length and patch area having little
effect on the overall large patch size. The implementation of this particular edge
management technique on P. sitchensis patches of this size would do little to increase
edge habitat and therefore encourage invertebrate species diversity. However the
application of bays to the P. sitchensis patches resulted in a significant increase in edge
habitat particularly when cut at high densities, the affect being even more dramatic if patch size was reduced. The best method therefore for maximising invertebrate diversity within *P. sitchensis* patches in Kielder Forest, Northumberland, would be to implement the cutting of high density bays into the patches and over time reduce patch size within the landscape.

Again, in the same way that the two tree species responded differently in their edge-effects, they showed different patterns in their proportion of edge and core habitat a result of the different sizes of patch area. *Pinus sylvestris* unlike *Picea sitchensis* tends to be planted in smaller patches as it grows in drier more lowland areas where space is at a premium. The smaller patch size of *P. sylvestris* has a significant effect on the quantity of core habitat present in the patches, which is particularly important to the level of invertebrate diversity within the species which is reliant on core habitat. The core-area model calculated low quantities of core habitat in the *P. sylvestris* research patches, at times as little as 0.5 of a hectare. This is a small area to support minimum viable populations even for invertebrates (Mader 1984, Muhlenberg *et al.* 1991) and could be susceptible to catastrophic exposure events which can be seen by its response to edge management (see below).

With the implementation of both types of edge management the levels of core habitat in the *P. sylvestris* patches were significantly reduced, at times the whole patch exposed to edge-effects resulting in no core habitat. This loss of core habitat would be associated with a significant reduction in the diversity of the invertebrate community within the
plantation patch, including some important forest specialist species. Therefore edge management should not be considered an appropriate management activity in *P. sylvestris* plantation patches of a small size if invertebrate species richness is to be encouraged. Rather a process of patch and edge protection should be implemented such as the development of buffer zones (Schonewald-Cox and Bayless 1986) or the increase in the average plantation patch size.

In general the core-area model (Laurance and Yensen 1991) coped well in this instance with the field data collected for canopy invertebrates and was quick and easy to perform making it a potentially useful tool for habitat managers. The model is especially useful as a tool for assessing the effects of management techniques, specifically those resulting in changes in edge-effect depth or patch shape on habitat patches, before management is applied reducing the likelihood of habitat damage due to ill-advised management.

Chapter 5 explored variations in the invertebrate communities associated with the two tree species resulting from differences in their structure, chemistry, length of time in the flora and land area coverage. Invertebrate communities are unique to plant species even those of the same genus (Southwood *et al.* 1982 a and b, Basset *et al.* 1996) herbivorous species being particularly so. This development of a specific community on plants, which is established whilst they are young, is a response to plants' abiotic and biotic conditions. Variation in structural complexity within plants results in different habitat niches, this has been found to be particularly important to spider species whose abundance is reduced with a reduction in structural complexity of plants (Watt *et al.* 1997). Specific Araneae
species also require certain structural spaces within the habitat in which to build their webs, sheetweb spiders preferring low conifer needle density providing more open areas for web construction (Gunnarsson 1988), whilst Theridiidae the scaffold-web builders prefer high needle density capable of supporting their complex webs (Gunnarsson 1988). Plant chemistry has a profound effect on invertebrate communities, the more complex and toxic the chemistry of the plant the less invertebrate species are capable of utilising it as a food source (Speight and Wainhouse 1989). Invertebrate species either choose not to feed on the plant or select areas of low chemical concentration, for example the jack pine budworm chooses to feed in the basal areas of needles where nutrient content is low associated with reduced defensive chemicals (Wallin and Raffa 1998).

If a plant has been present in a flora for a considerable time invertebrate species have had time to adjust to its chemistry and lifecycle, it may therefore be expected that a recent introduction to a flora will have a less complex community than that of a native species. In a similar way a plant’s abundance affects the diversity of the community present on it, if a plant has a low density and is widely distributed it will have a reduced invertebrate community as movement between the various populations is difficult due to the distance. However an abundant and closely distributed plant species will have a more complex invertebrate community as populations can become large and maintain contact reducing localised extinctions of populations.

Both tree species studied are important in the UK flora for different reasons, *Pinus sylvestris* is the only native conifer and has therefore been in the flora for a considerable
time, the species should therefore have a complex community supporting nationally important species. In contrast *Picea sitchensis*, a recent introduction, has become the most commonly planted tree in the UK covering large areas of northern England, Wales and Scotland. It would be expected that *P. sitchensis* supports a less diverse community than *P. sylvestris*, particularly its herbivores, because it is introduced however this factor may be balanced by the high density of the tree within the landscape, being very apparent to invertebrate species and thus encouraging their use of the habitat. Information on the developing *P. sitchensis* invertebrate community is vital to see whether the species is capable in time of supporting a rich invertebrate community containing nationally important forest species.

Clear differences were seen in the invertebrate communities between the two tree species even though the trees were of a similar age, height and planted under similar regimes, these differences being a result of the species’ structures and history in the UK. Variations occurred in invertebrates in densities, species richness and the species present, the overall pattern being a less dense but more diverse invertebrate community in *P. sylvestris* compared to a community made up of a few highly abundant invertebrates in *P. sitchensis*.

The higher species richness in *P. sylvestris* was a result of high coleopteran, araneid and tourist species diversity, this result supports the concept of a more diverse community with key forest specialist species occurring on more native plant species. The *P. sylvestris* community should have more herbivorous species than that of *P. sitchensis*, species
having had time to adapt to the chemistry of the pine. Detritivores of the community should also be limited due to a reduced epiphyte load in the canopy a result of the warmer and more open conditions of the canopy. The native pine with its diverse understory supported many tourist species e.g. Ephemeroptera and Tricoptera, using the canopy as a resting site whilst utilising other areas of the forest system, the canopy also had high coleopteran diversity a mixture of both predatory and herbivore species with a few key herbivore species. Detritivore species such as the Collembola and Acarina showed similar richness to *P. sitchensis* but were generally less important a constituent of the community reflecting the reduced epiphyte load and standing dead organic matter of *P. sylvestris*.

The beetle community of *P. sitchensis* was relatively limited and was dominated by the predatory Coccinellidae feeding on the abundant aphid community of the canopy. *Pinus sylvestris* supported a complex coleopteran community of predatory species associated with many prey items and a herbivorous beetle community adapted to the chemistry of the pine. Increased coleopteran richness has been reported in more open canopy habitats such as in *P. sylvestris* (Greatorex-Davies *et al.* 1994) however a similar study in UK conifers found increased beetle diversity in *P. sitchensis* (Ozanne 1991). This may suggest that the response to *P. sylvestris* habitat is not consistent in the Coleoptera, but is associated more with the region the samples are taken from. In the present research the *P. sitchensis* samples were taken from the north of England unlike the Ozanne (1991) samples collected in Wales, the more northerly sample area of the present study could be limiting beetle diversity due to the cooler regional climate. Few key forest specialist species appeared to be supported by the *P. sitchensis* habitat however *P. sylvestris*
supported two particularly sensitive spider species in its core habitat, *Drapetisca socialis* and *Leptophantes expunctus*.

*Picea sitchensis* supported a much simpler yet slightly more abundant community than *P. sylvestris* mainly dominated by epiphytic and detritivore feeders. The Collembola and Acarina dominated the *P. sitchensis* community thriving in the cool, moist conditions which support high epiphytic growth. Although species richness of the two orders was slightly higher in *P. sitchensis* the figures were relatively low compared to studies in old growth Sitka spruce, a result of the managed habitat being held in an early successional state, epiphytic diversity increasing with habitat age (Pettersson *et al.* 1995, Esseen *et al.* 1996). The recent history of *P. sitchensis* in the flora of the UK appears to be outweighing the dominance of its planting within the country, causing it to have a simplified canopy community compared to the native *P. sylvestris*. However invertebrate species are inhabiting the canopy and more seem to be extending their range to include introduced conifer species (Fraser and Lawton 1994).

The research has shown that the two conifer species studied support a diverse and abundant canopy invertebrate community, which is unique to each species. *Pinus sylvestris* supports a diverse community, including nationally important forest specialists (e.g. *Drapetisca socialis*), and this occurs predominantly in the core area of the patches. To maximise overall invertebrate richness and important species specifically, edge management techniques suggested for improving invertebrate diversity within plantations should not be implemented within *P. sylvestris* plantations. In general the average small
size of *P. sylvestris* patches resulted in excessive reduction or loss of the key core habitat, therefore management to protect core habitat from edge exposure either by buffer zones or increasing patch size should be implemented.

Further to this it has been shown that the canopy of *P. sitchensis* is not as dark and barren as it is sometimes considered but actually supports an ever increasing community of invertebrate species. Implementation of proposed edge management techniques will increase edge habitat within the landscape improving the capacity of these widespread plantations to support a full and diverse invertebrate community, which could eventually gain nationally important species.

The use of canopy invertebrate communities in this research has highlighted the occurrence of edge-effects within UK conifers beyond the distance previously studied, supporting findings of edge-effect depths greater than 50 metres in other forest habitats. The data emphasise the need to study edge-effects beyond 50 metres in all habitat types and that patterns recorded in one species may not necessarily be the same as in another tree species, even grown under similar conditions. Generalisation of edge-effect depths should not be made across tree species, however some patterns within tree species appear to be consistent between studies performed years apart, both Collembola and Araneae responding similarly in the present research and in Ozanne (1991).

Although new techniques for edge-effect detection have been developed they may prove of limited use across relatively small scale edges and visual detection of edge-effect
depths is still a passable way of defining them in the context of the calculation of core area proportions. Core-area models have been shown to be an excellent tool in assessing the quality of habitat patches for supporting key communities and are simple and quick for habitat managers to use. However reliance on 50% desired habitat as a key management aim is ill-advised, instead attention should be paid to the actual quantity of available habitat and its relation to minimum viable population levels.

Overall conifer plantations in the UK are an ever increasing and biologically interesting habitat for invertebrate species. This research shows that implementation of two different basic management techniques within *Pinus sylvestris* and *Picea sitchensis* should encourage invertebrate communities, improving the conservation value of the habitat and its future potential for housing important forest biotic resources.
Reference List.


Appendix 1. Numbers of taxa caught in 1m² drop trays against distance (metres) from plantation edge in transect NY 1 *Pinus sylvestris*.

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Appendix 2. Numbers of taxa caught in 1m² drop trays against distance (metres) from plantation edge in transect NY 2, *Pinus sylvestris*.

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[^1]: Further details and notes on methodology and data collection would be added here.
Appendix 4. Numbers of taxa caught in 1 m$^2$ drop trays against distance (metres) from plantation edge in transect KM 1 Picea sitchensis.

| Taxa          | 0m  | 5m  | 10m | 15m | 20m | 25m | 30m | 35m | 40m | 45m | 50m | 55m | 60m | 65m | 70m | 75m | 80m | 85m | 90m | 95m | 100m | 105m | 110m | 115m | 120m |
|---------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Acatrina      | 252 | 375 | 405 | 246 | 215 | 210 | 206 | 193 | 170 | 287 | 265 | 283 | 335 | 345 | 453 | 456 |
| Araneae       | 20  | 41  | 54  | 42  | 49  | 31  | 28  | 16  | 16  | 17  | 17  | 18  | 19  | 23  | 21  | 22  | 22  | 16  | 11  | 7   | 4   | 1   |
| Coleoptera    | 75  | 75  | 75  | 75  | 50  | 12  | 12  | 12  | 12  | 95  | 175 | 175 | 650 | 456 | 456 | 298 | 298 | 715 | 370 | 415 | 800 | 508 |
| Diptera       | 11  | 71  | 50  | 12  | 18  | 31  | 44  | 44  | 44  | 44  | 44  | 44  | 44  | 44  | 44  | 44  | 44  | 44  | 44  | 44  | 44  | 44  |
| Hymenoptera   | 7   | 1   | 2   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   |
| Neuroptera    | 2   | 1   | 1   | 2   | 1   | 2   | 2   | 2   | 2   | 2   | 2   | 2   | 2   | 2   | 2   | 2   | 2   | 2   | 2   | 2   | 2   | 2   |
| Opilionidae   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   |
| Psocoptera    | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   |
| Thysanoptera  | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   |
Appendix 5. Numbers of taxa caught in 1m² drop trays against distance (metres) from plantation edge in transect KM 2 *Picea sitchensis*.

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**Appendix 7.** Numbers of taxa caught in 1m² drop trays against distance (metres) from plantation edge in transect KM 4 *Picea sitchensis*.

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